LARVAL FISH DYNAMICS IN THE SHALLOW NEARSHORE OF EASTERN ALGOA BAY WITH PARTICULAR EMPHASIS ON THE EFFECTS OF CURRENTS AND SWIMMING ABILITIES ON DISPERSAL

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GENERAL ABSTRACT

The larval fish assemblage in the shallow, nearshore region of a proposed marine protected area (MPA) in eastern Algoa Bay, temperate South Africa was investigated. Current velocities and direction and the swimming abilities of late-stage larvae were further assessed to determine potential larval movement to and from the MPA. In total, 6045 larval fishes were collected along two depth contours (~5m and ~15m) in the shallow nearshore of eastern Algoa Bay using stepped-oblique bongo net tows, twice per season for two years (March 2005 – January 2007). These larvae represented 32 families and 78 species. The Gobiidae, Cynoglossidae, Clupeidae, Engraulidae and Sparidae were the dominant fish families. Catches varied significantly between seasons peaking in spring with a mean of 64 larvae/100m^3. Preflexion stage larvae dominated catches (75%). All developmental stages of *Diplodus capensis*, *Engraulis capensis*, *Heteromycteris capensis*, *Sardinops sagax* and *Pomadasys* species were found in the study area. It appears that these species use the shallow nearshore as a nursery area. Analysis of 12 months (May 2006 – May 2007) data from a bottom-moored Acoustic Doppler Current Profiler within the study area showed that offshore south eastward (39%) and onshore north westward currents (33%) dominated. The south westward current (15%) and north eastward current (12%) occurred less frequently. Current velocity decreased with depth in the nearshore, with a mean velocity of ~29 cms^{-1} recorded at a depth of 4 m and a mean velocity of ~11 cms^{-1} recorded at a depth of 14 m. Understanding the dispersal and movement of marine fish larvae in coastal habitats requires knowledge of active swimming abilities. The critical speed and endurance swimming of late stage larvae of two common inshore species occurring in the study area, *Diplodus capensis* and *Sarpa salpa* (Family Sparidae), were measured in a laboratory swimming chamber. The mean *U*-crit value for *D. capensis* (18.6 cms^{-1}) was similar to that of *S. salpa* (18.0 cms^{-1}), whereas mean endurance (km swum) was greater in *S. salpa* (8.4 km) than *D. capensis* (5.9 km). These swimming abilities exceed the average current velocities observed in the shallow nearshore providing larvae with the ability to greatly alter their passive dispersal trajectories and ultimately influence their distribution in the nearshore.

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DECLARATION

The following thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author.

CHAPTER 1

GENERAL INTRODUCTION

1. AN OVERVIEW OF MARINE LARVAL FISH RESEARCH IN SOUTH AFRICA

1.1 Larval fish descriptions

1900 – 1970

Descriptions of marine ichthyoplankton in South Africa first began with the pioneering work of Gilchrist in the early 1900's with isolated annotations on the eggs and larvae of some Cape fishes (Gilchrist, 1903; Gilchrist, 1904; Gilchrist, 1916; Gilchrist and Hunter, 1919; Gilchrist, 1921). On the west coast of South Africa, the larval stages of *Merluccius capensis* (Family: Merlucciidae), *Thyrsites atun* (Family: Gempylidae) and *Helicolenus dactylopterus* (Family: Scorpaenidae) three economically important fish species in South Africa, were described and their distribution investigated between 1950 and 1967 (De Jager, 1955; Haigh, 1972).

1971 – 1980

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). King et al. (1978) observed time of hatching and size at hatching from laboratory rearing experiments on *E. capensis*. The eggs and larval stages of the commercially important west coast sole, *Austroglossus microlepis* (Family: Soleidae), were also described in the late 1970's (O'Toole, 1977). 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).

1981 – 1990

The eggs and larval development of artificially spawned southern mullet, *Liza richardsonii* (Family: Mugilidae) were described to an age of 46 days (Cambray and Bok, 1989). The larval development of the important linefish sciaenid *Argyrosomus japonicus* and the sparid *Spondyliosoma emarginatum* were described from wild caught specimens (Beckley, 1989; Beckley, 1990).

1991 – present

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). These included species from the orders Anguilliformes, Aulopiformes, Batrachoidiformes, Clupeiformes, Cyprinodontiformes, Elopiformes, Gadiformes, Gobiesociformes, Gonorynchiformes, Myctophiformes, Ophidiiformes, Perciformes, Pleuronectiformes, Salmoniformes, Scorpaeniformes, Stomiiformes and Zeiformes. In addition to the descriptions of the early developmental stages of species from these orders inhabiting the Benguela region, the spawning areas and seasons were reported. On the east coast of South Africa, in the region of the Agulhas Current, Myctophidae larvae from the genera *Benthosema*, *Diogenichthys*, *Myctophum*, among others, were described (Olivar and Beckley, 1995; Olivar et al., 1999). The larval stages of species from the order Perciformes including *Argyrozona argyrozona* (Davis and Buxton, 1996), *Dichistius capensis* (Leis and van der Lingen, 1997), *Cheimerius nufar* (Connell et al., 1999) and *Pagellus natalensis* (Leis et al., 2002) and species from the order Pleuronectiformes including *Austroglossus pectoralis* (Wood, 2000), *Cynoglossus zanzibarensis* (Wood, 2003) and *Dagetichthys marginatus* (Thompson et al., 2007) have also been described in more recent times.

1.2 Offshore assemblages

A larval fish survey was conducted by the Sea Fisheries Branch on the west coast of South Africa in 1972 (O'Toole, 1974). The purpose of this survey was to investigate the time of spawning and geographical limits *of S. sagax* (Family: Clupeidae) *E. capensis* (Family: Engraulidae) and *Trachurus trachurus* (Family: Carangidae), as a method of stock assessment for these commercially important pelagic species. This survey also gathered information on the distribution, abundance and ecology of the larval stages of *Austroglossus microlepis* (Family: Soleidae), *Dicloglossa cuneata*

(Family: Soleidae), *Sufflogobius bibarbatus* (Family: Gobiidae), *M. capensis* (Family: Merlucciidae) and other mesopelagic species.

Several research cruises along the east coast of South Africa were conducted by the Sea Fisheries Branch between 1951 – 1969 to investigate the spawning of *E. capensis* and *S. sagax* (Anders, 1975). The eggs of *S. sagax* collected during these surveys were observed to coincide with the annual "Sardine Run" which occurs in June or early July on the east coast of South Africa. This study represents the first published ecological study on marine ichthyoplankton from the subtropical east coast of South Africa (Anders, 1975).

During the early 1980's the spawning and transport of *E. capensis* eggs and larvae via shelf-edge frontal jet currents in the vicinity of Cape Point received much research attention (Badenhorst and Boyd, 1980; Shelton and Hutchings, 1981; Shelton and Hutchings, 1982; Shelton, 1984). The spawning period of the inshore blenniid, *Parablennius cornutus*, and size at hatching was reported in KwaZulu-Natal (Eyberg, 1984).

The second ichthyoplankton survey on the east coast of South Africa occurred in the region of the Agulhas Current (Beckley and Van Ballegooyen, 1992). The spatial and temporal distributions of lanternfish and scombrid larvae were analyzed from this ichthyoplankton survey. The greatest densities of lanternfish larvae occurred close inshore (50 – 100 m deep) and was related to the shoreward intrusions of the Agulhas Current surface water (Olivar and Beckley, 1994). Scombrid larvae showed distinct spatial and temporal variation in distribution and abundance off the east coast of South Africa and could be linked to seasonal oceanographic conditions (Beckley and Leis, 2000).

1.3 Surf zone assemblages

The first surf zone studies in South Africa described assemblages of juvenile fishes and found these habitats to function as nursery areas for some species of coastal fishes (Lasiak, 1981; Lasiak, 1986; Bennett, 1989). The first larval fish study in a South African surf zone assessed the use of this habitat as a nursery area for estuary dependent marine fish species (Whitfield, 1989a). Only one study on larval fishes in the surf zone has been conducted in subtropical KwaZulu-Natal (Harris and Cyrus, 1996). Most work to date has taken place in warm temperate waters. In the temperate surf zones of the Eastern Cape, the ichthyoplankton assemblage adjacent to the mouth of an intermittently open estuary was investigated and the estuarine immigration of larvae during marine overwash events was observed (Cowley et al., 2001). The investigation into the larval and early juvenile fishes in the surf zone adjacent to two intermittently open estuaries in temperate South Africa suggested that estuary/river water that enters the surf zone creates an accumulation response by larvae of estuary associated fishes (Strydom, 2003). The habitat use by larval fishes was investigated in a temperate surf zone and it was shown that larvae actively select areas of reduced current flow in depressions associated with dissipative beach surf zones (Watt-Pringle and Strydom, 2003). A study of larval fishes in a non-estuary associated surf zone provided evidence that these assemblages are linked by estuary associated larvae occurring in surf water irrespective of proximity to estuary mouths (Strydom and d'Hotman, 2005).

1.4 Nearshore assemblages

The first larval fish study on the composition of marine ichthyoplankton assemblages in the shallow nearshore was conducted in the western sector of Algoa Bay in the Eastern Cape (Beckley, 1986). Beckley (1986) discussed the various taxa occurring in the ichthyoplankton in terms of the distribution of adults and juveniles, the breeding biology and available literature on the early life history of these species. Low abundances of larvae from coastal species that spawn pelagic eggs including sciaenids, soleids and sparids occurred within the study area suggesting that spawning and development occurs away from the nearshore region (Beckley, 1986). This was followed by a study on the composition of larvae occurring in the Tsitsikamma National Park on the temperate south east coast of South Africa (Tilney and Buxton, 1994; Tilney et al., 1996). This ichthyoplankton study formed part of a broader study to investigate the role played by the Tsitsikamma National Park marine reserve in seeding adjacent, fished areas with eggs and larvae. Recently, a 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 shallow nearshore waters with larger individuals occurring in the surf.

In sub-tropical KwaZulu-Natal, two nearshore larval fish studies have taken place (Harris et al., 1999; Harris et al., 2001). The purpose of the first study (Harris et al., 1999) was to describe the composition of larval fish assemblages in the St Lucia nearshore and compare catches with those occurring in the St Lucia Estuary (Harris and Cyrus, 1995) and adjacent surf zone (Harris and Cyrus, 1996). The second nearshore study assessed assemblages of larval fishes along an ocean-estuarine gradient and related these to the physical characteristics of each environment (Harris et al., 2001).

2. RATIONALE FOR THIS STUDY

Coastal habitats such as nearshore waters and bays, surf zones and estuaries are known to serve as important areas for the development of the early stages of many marine fish species (Senta and Kinoshita, 1985; Beckley, 1986; Lasiak, 1986; Boehlert and Mundy, 1988; Whitfield, 1989a; Potter et al., 1990; Raynie and Shaw, 1994; Strydom et al., 2003; Hernández-Miranda et al., 2003). Surf zones also play an important role as accumulation areas and transient routes for the postflexion and settlement stages of mainly estuary associated species (Senta and Kinoshita, 1985; Boehlert and Mundy, 1988; Whitfield, 1989a; Doherty and McIlwain, 1996; Cowley et al., 2001; Strydom and d'Hotman, 2005). In South Africa, many commercially and recreationally important marine species breed at sea with the postflexion larvae and early juveniles recruiting from nearshore and offshore spawning grounds into estuarine nursery areas (Whitfield, 1989b; Harris and Cyrus, 1995; Harris et al., 1995; Strydom et al., 2003), so much so that these fishes have been categorized according to their degree of dependence on estuaries (Whitfield, 1998). At present, the occurrence, abundance and distribution of the preflexion stages of these estuary associated marine species is poorly understood, highlighting the lack of nearshore research in South Africa.

In South Africa, nearshore research on larval fishes is confined to two studies conducted in subtropical KwaZulu-Natal (Harris et al., 1999; Harris et al., 2001) and three studies in the warm temperate Eastern Cape (Beckley, 1986; Tilney and Buxton, 1994; Strydom, 2007). International studies define the shallow nearshore as that close to shore before the surf zone in direction to the shoreline in depths of <15 m (Hernández-Miranda et al., 2003; Azeiteiro et al., 2006). Internationally, research on shallow (<15 m) nearshore larval fishes is similarly lacking (Palomera and Olivar, 1996; Azeiteiro et al., 2006; Sabatés et al., 2007). Several studies however have concentrated on larval fish assemblages in nearshore coastal waters over the continental shelf where depths far exceed 15 m (Kingsford and Choat, 1989; Tricklebank et al., 1992; Cowen et al., 1993; Chiu and Hsyu, 1994; Hutchins and Pearce, 1994; Sponaugle et al., 2002). Studies have found that the spawning mode of adults plays a key role in determining the composition of nearshore ichthyoplankton communities (Leis and Miller, 1976). In South Africa, coastal species producing benthic eggs dominate catches in the western sector of Algoa Bay (Beckley, 1986), while on exposed coasts such as the Tsitsikamma National Park (Tilney and Buxton, 1994) and the subtropical nearshore waters of KwaZulu-Natal (Harris et al., 1999), larvae from pelagic species spawning pelagic eggs dominate catches.

Currents are known to play an important role in determining the distribution of larval fishes in the ocean (Leis and Goldman, 1983). However, an understanding of shallow water current dynamics is lacking. No detailed oceanographic research on current direction and velocity in shallow nearshore waters is available as offshore oceanography has taken precedence (Harris, 1978; Lutjeharms et al., 1986; Goschen and Schumann, 1988; Boyd et al., 1992; Goschen and Schumann, 1994; Boyd and Oberholster, 1994). In Algoa Bay all past studies have been concentrated in the western sector of the bay (CSIR, 1970; Roberts, 1990). One South African research paper has described current dynamics in the Tsitsikamma National Park and also included an assessment of the potential transport of squid paralarvae and ichthyoplankton spawned within the park (Roberts and van den Berg, 2005). These results all suggest that fish larvae and squid paralarvae are exported beyond the boundaries of that park. Providing adjacent fished areas with larval recruits is an important objective of Marine Protected Areas (MPAs) (Jennings, 2000; Leis, 2003). In more recent times the importance of coastal habitats, particularly declining fish stocks, has come to the fore. Increasing pressure to provide conservation status to coastal resources has led to the proposal of MPAs.

Before establishing MPAs, it is essential to understand the influence of current flow patterns in distributing larval fishes to adjacent fished areas. The present study will provide more information on current direction and velocity occurring in a proposed new MPA in the eastern sector of Algoa Bay which will be used to describe possible dispersal and movement of eggs and larval fishes within the area. The extent of dispersal has important implications on the design of MPAs in terms of size and location as the geographical extent of populations is linked to the larval phase.

International research has shown that the behaviour of larval fishes influences dispersal beyond that which is predicted by local current regimes (Armsworth et al., 2001; Leis, 2006). Therefore the size at which larvae exhibit active swimming and the magnitude of this swimming ability needs to be assessed in order to determine how susceptible larvae are to passive transport by local current regimes. Studies on the swimming abilities of larval fishes have shown that most larvae are strong swimmers, capable of swimming speeds greater than that observed in local current regimes (Leis and Stobutzki, 1999; Dudley et al., 2000; Fisher and Bellwood, 2002; Fisher and Bellwood, 2003; Fisher, 2005; Leis et al., 2006). These swimming abilities allow larvae to actively influence their trajectories and can therefore regulate their horizontal and vertical distribution in the water column. No previous studies have assessed larval fish swimming abilities in South Africa. This study represents the first assessment of the swimming abilities of two species of late-stage Sparidae larvae, which have important recreational fishing value. This study will provide invaluable insight into how susceptible larvae are to local currents in Algoa Bay and should lead the way for future studies on the influence of larval behaviour on dispersal and movement. A better understanding of the behavioural abilities of larvae will allow for more realistic models of larval dispersal to be generated (Stobutzki, 2001). Determining the influence of larval fish behaviour on dispersal and population connectivity is a relatively new field of research (Bellwood et al., 1998), and has not been attempted in South Africa. Knowledge of the scale of dispersal of eggs and larvae of fishes requiring conservation, will allow for the correct location and size of MPAs to be determined within specific coastal regions of the country.

Given the lack of nearshore research both on larval fishes and shallow current dynamics, the proposal of a new MPA in the eastern sector of Algoa Bay provided the ideal opportunity to generate new information on species composition, seasonality, distribution and abundance as well as the potential effect of currents on eggs and larvae in the area. As international research has shown that behaviour of larval fishes plays an important role in determining dispersal trajectories, the swimming abilities of late-stage larvae of two common inshore South African species were studied in order to evaluate their susceptibility to dispersal via local current flow through the MPA.

3. OBJECTIVES AND AIMS

The objective of this research was to conduct a two-year study on the larval fish assemblage in the shallow nearshore of the proposed Greater Addo Marine Reserve (GAMR) in the eastern sector of Algoa Bay in order to provide more information on larval fish dynamics in the nearshore and to put this information into perspective with what is known about larval fishes occurring in adjacent surf zones and estuaries. In addition, shallow water currents were measured to further understand the direction and velocity of water flow in the larval environment. Assessments on the swimming abilities of two common inshore linefish species were also made in order to comment on potential dispersal and movement in the study area relative to current flow patterns.

The aims of the present study were to determine the:

- Composition, distribution, abundance, seasonality and developmental stages of larval fishes occurring along two different depth contours in the shallow nearshore region of the proposed GAMR (Chapter 2)
- Shallow water current flow patterns in the nearshore of the proposed GAMR (Chapter 3)
- Swimming abilities of late stage Sparidae larvae belonging to two common inshore species, *Diplodus capensis* and *Sarpa salpa* occurring in the shallow nearshore region of the GAMR (Chapter 4).

4. REFERENCES CITED

ANDERS, A.S. 1975. Pilchard and anchovy spawning along the Cape east coast. *South African Shipping News and Fishing Industry* **30**: 53-57.

ARMSWORTH, P.R., MAURICE, K.J., BODE, L. 2001. Dispersal strategies for reef fish larvae. *Am Nat* **157**: 434-450.

AZEITEIRO, U.M., BACHELAR-NICOLAU, L., RESENDE, P., GONÇALVES, F., PEREIRA, M.J. 2006. Larval fish distribution in shallow coastal waters off North Western Iberia (NE Atlantic). *Estuarine, Coastal and Shelf Science* **69**: 554-566.

BADENHORST, A., BOYD, A.J. 1980. Distributional ecology of the larvae and juveniles of the anchovy *Engraulis capensis* Gilchrist in relation to the hydrological environment off South West Africa. *Fishery Bulletin of South Africa* **13**: 83-106.

BECKLEY, L.E. 1986. The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. *South African Journal of Zoology* **21**: 244-252.

BECKLEY, L.E. 1989. Larval development of *Spondyliosoma emarginatum* (Cuvier & Valenciennes) (Pisces: Sparidae) from southern Africa. *South African Journal of Zoology* **24**: 187-192.

BECKLEY, L.E. 1990. The description of the early life history stages of the kob, *Argyrosomus holoeipidotus* (Pisces: Sciaenidae), from southern Africa. *South African Journal of Zoology* **25**: 224-228.

BECKLEY, L.E., LEIS, J.M. 2000. Occurrence of tuna and mackerel larvae (Family: Scombridae) off the east coast of South Africa. *Marine and Freshwater Research* **51**: 777-782.

BECKLEY, L.E., VAN BALLEGOOYEN, R.C. 1992. Oceanographic conditions during three ichthyoplankton surveys of the Agulhas Current in 1990/91. *South African Journal of Marine Science* **12**: 83-93.

BELLWOOD, D.R., LEIS, J.M., STOBUTZKI, I.C. 1998. Fishery and reef management. *Science* **279**: 2021-2022.

BENNETT, B.A. 1989. The fish community of a moderately exposed beach on the southwestern Cape coast of South Africa and an assessment of this habitat as a nursery for juvenile fish. *Estuarine, Coastal and Shelf Science* **28**: 293-305.

BOEHLERT, G.W., MUNDY, B.C. 1988. Roles of behaviour and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* **3**: 51-67.

BOYD, A.J., OBERHOLSTER, G.P.J. 1994. Currents off the west and south coasts of South Africa. *South African Shipping News and Fishing Industry* September/October: 26-28.

BOYD, A.J., TAUNTON-CLARK, J., OBERHOLSTER, G.P.J. 1992. Spatial features of the near-surface and midwater circulation patterns off western and southern South African and their role in the life histories of various commercially fished species. *South African Journal of Marine Science* **12**: 189-206.

BROWNELL, C.L. 1979. Water quality requirements for first-feeding in marine fish larvae of the Cape of Good Hope, with descriptions of developmental stages. Ph.D. thesis University of Cape Town, South Africa 272pp, CAMBRAY, J.A., BOK, A.H. 1989. Early development of artificially spawned southern mullet, *Liza richardsonii* (Smith, 1986). *South African Journal of Zoology* **24**: 193-198.

CHIU, T.S., HSYU, Y.I. 1994. Interannual variation of ichthyoplankton density and species composition in the waters off northeastern Taiwan. *Marine Biology* **119**: 441-448.

CONNELL, A.D., HEEMSTRA, P.C., GARATT, P.A. 1999. Eggs and larvae of the santer *Cheimerius nufar* (Perciformes: Sparidae) from KwaZulu-Natal, South Africa. *South African Journal of Marine Science* **21**: 41-50.

COWEN, R.K., HARE, J.A., FAHAY, M.P. 1993. Beyond hydrography: can physical processes explain larval fish assemblages within the middle Atlantic Bight? *Bulletin of Marine Science* **53**: 567-587.

COWLEY, P.D., WHITFIELD, A.K., BELL, K.N.I. 2001. The surf zone ichthyoplankton adjacent to the mouth of a predominantly closed southern African estuary, with evidence of recruitment during marine overwash events. *Estuarine, Coastal and Shelf Science* **52**: 339-348.

CSIR 1970. Algoa Bay coastal erosion investigation. Parts I and II. Hydraulic Research Unit, NMERI, CSIR, Stellenbosch, MEG 913 and 914.

DAVIS, J.A., BUXTON, C.D. 1996. Larval development of laboratory-reared carpenter, *Argyrozona argyrozona* (Pisces: Sparidae). *South African Journal of Zoology* **31**: 10-14.

DE JAGER, B.V.D. 1955. The South African pilchard (*Sardinops ocellata*). The development of the snoek (*Thyrsites atun*), a fish predator of the pilchard. *Investigational Report of the Division of Fisheries of the Union of South Africa* **19**: 1-16.

DOHERTY, P., MCILWAIN, J. 1996. Monitoring larval fluxes through the surf zones of Australian coral reefs. *Marine and Freshwater Research* **47**: 383-390.

DUDLEY, B., TOLIMIERI, N., MONTGOMERY, J.C. 2000. Swimming ability of the larvae of some reef fishes from New Zealand waters. *Marine and Freshwater Research* **51**: 783-787.

EYBERG, I. 1984. The biology of *Parablennius cornutus* (L.) and *Scartella emarginata* (Günther) (Teleostei: Blenniidae) on a Natal reef. *Investigational Report of the Oceanographic Research Institute* **54**: 1-16.

FISHER, R. 2005. Swimming speeds of larval coral reef fishes: implications on self-recruitment and dispersal. *Marine Ecology Progress Series* **285**: 223-232.

FISHER, R., BELLWOOD, D.R. 2002. The influence of swimming speed on sustained swimming performance of late-stage reef fish larvae. *Marine Biology* **140**: 801-807.

FISHER, R., BELLWOOD, D.R. 2003. Undisturbed swimming behaviour and nocturnal activity of coral reef fish larvae. *Marine Ecology Progress Series* **263**: 177-188.

GILCHRIST, J.D.F. 1903. The development of South African fishes. Part I. *Marine Investigations in South Africa* **2**: 181-201.

GILCHRIST, J.D.F. 1904. The development of South African fishes. Part II. *Marine Investigations in South Africa* **3**: 131-150.

GILCHRIST, J.D.F. 1916. Eggs and larvae of Cape fishes. Province of the Cape of Good Hope. *Union of South Africa Marine Biological Report* **3**: 1-26.

GILCHRIST, J.D.F. 1921. Reproduction of deep sea fishes. *Annals and Magazine of Natural History* **9**: 173-177.

GILCHRIST, J.D.F., HUNTER, H. 1919. Reproduction of the fishes in Table Bay. *Transactions of the Royal Society of South Africa* **8**: 1-13.

GOSCHEN, W.S., SCHUMANN, E.H. 1988. Ocean current and temperature structures in Algoa Bay and beyond in November 1986. *South African Journal of Marine Science* **7**: 101-116.

GOSCHEN, W.S., SCHUMANN, E.H. 1994. An Agulhas Current intrusion into Algoa Bay during August 1988. *South African Journal of Marine Science* **14**: 47-57.

HAIGH, E.H. 1972. Larval development of three species of economically important South African fishes. *Annals of the South African Museum* **59**: 47-70.

HARRIS, S.A., CYRUS, D.P. 1995. Occurrence of larval fishes in the St Lucia Estuary, KwaZulu-Natal, South Africa. *South African Journal of Marine Science* **16**: 333-350.

HARRIS, S.A., CYRUS, D.P. 1996. Occurrence of larval fish in the surf zone adjacent to the St Lucia Estuary mouth, KwaZulu-Natal, South Africa. *Marine and Freshwater Research* **47**: 465-482.

HARRIS, S.A., CYRUS, D.P., BECKLEY, L.E. 1999. The larval fish assemblage in the nearshore coastal waters off the St Lucia Estuary, South Africa. *Estuarine, Coastal and Shelf Science* **49**: 789-811.

HARRIS, S.A., CYRUS, D.P., BECKLEY, L.E. 2001. Horizontal trends in larval fish diversity and abundance along an ocean-estuarine gradient on the Northern KwaZulu-Natal Coast, South Africa. *Estuarine, Coastal and Shelf Science* **53**: 221-235.

HARRIS, S.A., CYRUS, D.P., FORBES, A.T. 1995. The larval fish assemblage at the mouth of the Kosi Estuary, KwaZulu-Natal, South Africa. *South African Journal of Marine Science* **16**: 351-364.

HARRIS, T.F.W. 1978. Review of coastal currents in South African wasters. *South African National Scientific Programmes Report* **30**: 1-103.

HERNÁNDEZ-MIRANDA, E., PALMA, A.T., OJEDA, F.P. 2003. Larval fish assemblages in nearshore coastal waters off central Chile: temporal and spatial patterns. *Estuarine, Coastal and Shelf Science* **56**: 1075-1092.

HUTCHINS, J.B., PEARCE, A.F. 1994. Influence of the Leeuwin Current on recruitment of tropical reef fishes at Rottnest Island, Western Australia. *Bulletin of Marine Science* **54**: 245-255.

JENNINGS, S. 2000. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries* **10**: 209-231.

KING, D.P.F., ROBERTSON, A.A., SHELTON, P.A. 1978. Laboratory observations on the early development of the anchovy *Engraulis capensis* from the Cape peninsula. *Fisheries Bulletin of South Africa* **10**: 37-45.

KINGSFORD, M.J., CHOAT, J.H. 1989. Horizontal distribution patterns of presettlement reef fish: are they influenced by the proximity of reefs? *Marine Biology* **101**: 285-297.

LASIAK, T.A. 1981. Nursery grounds of juvenile teleosts: evidence from the surf zone of King Beach, Port Elizabeth. *South African Journal of Science* **77**: 388-390.

LASIAK, T.A. 1986. Juveniles, food and the surf zone habitat: implications for teleost nursery areas. *South African Journal of Zoology* **21**: 51-56.

LEIS, J.M. 2003. What does the larval fish biology tell us about the design and efficacy of marine protected areas. Aquatic protected areas: What works best and how do we know? Australian Society for Fish Biology, North Beach, WA pp. 170-180,

LEIS, J.M. 2006. Are larvae of demersal fishes plankon or nekton? *Advances in Marine Biology* **51**: 59-141.

LEIS, J.M., GOLDMAN, B. 1983. Studies on the biology of larval fishes in the Lizard Island area, Northern Great Barrier Reef. Proceedings: Inaugural Great Barrier Reef Conference James Cooke University Press, Townsville 221-225.

LEIS, J.M., HAY, A.C., TRNSKI, T. 2006. In situ ontogeny of behaviour in pelagic larvae of three temperate marine, demersal fishes. *Marine Biology* **148**: 655-669.

LEIS, J.M., MILLER, J.M. 1976. Offshore distributional patterns of Hawaiian fish larvae. *Marine Biology* **36**: 359-367.

LEIS, J.M., STOBUTZKI, I.C. 1999. Swimming performance of late pelagic larvae of coral-reef fishes: in situ and laboratory-based measurements. In "Proceedings of the 5th Indo-Pacific fish conference, Noumea 1997"(Seret, B. and Sire, J.Y. eds), Noumea 575-583.

LEIS, J.M., TRNSKI, T., BECKLEY, L.E. 2002. Larval development of *Pagellus natalensis* and what larval morphology indicates about relationships in the perciform fish family Sparidae (Teleostei). *Marine and Freshwater Research* **53**: 367-376.

LEIS, J.M., VAN DER LINGEN, C.D. 1997. Larval development and relationships of the perciform family Dichistiidae (=Coracinidae), the Galjoen fishes. *Bulletin of Marine Science* **60**: 100-116.

LOUW, E., O'TOOLE, M.J. 1977. Larval development of *Sardinops ocellata* (Pisces: Clupeidae). *Annals of the South African Museum* **72**: 125-145.

LUTJEHARMS, J.R.E., BAIRD, D., HUNTER, I.T. 1986. Seeoppervlak dryfgedrag aan die Suid-Afrikaanse suidkus in 1979. *South African Journal of Science* **82**: 324-326.

O'TOOLE, M.J. 1974. Fish larval investigations off South West Africa. *South African Shipping News and Fishing Industry* **29**: 53-59.

O'TOOLE, M.J. 1977. Development and distributional ecology of the larvae of the West Coast Sole *Austroglossus microlepis*. *Fisheries Bulletin of South Africa* **9**: 32-45.

OLIVAR, M.P., BECKLEY, L.E. 1994. Influence of the Agulhas Current on the distribution of lanternfish larvae off the southeast coast of Africa. *Journal of Plankton Research* **16**: 1759-1780.

OLIVAR, M.P., BECKLEY, L.E. 1995. Early development of *Diaphus* spp. (Pisces: Myctophidae) of the Agulhas Current. *South African Journal of Marine Science* **16**: 129-139.

OLIVAR, M.P., FORTUÑO, J.M. 1991. Guide to ichthyoplankton of the southeast Atlantic (Benguela Current Region). *Sciencia Marina* **55**: 1-383.

OLIVAR, M.P., MOSER, H.G., BECKLEY, L.E. 1999. Lanternfish larvae from the Agulhas current (SW Indian Ocean). *Sciencia Marina* **63**: 101-120.

PALOMERA, I., OLIVAR, M.P. 1996. Nearshore ichthyoplankton off the Costa Brava (northwest Mediterranean Sea). *Publicaciones Especiales de Instituto Español de Oceanografía* **22**: 71-75.

POTTER, I.C., BECKLEY, L.E., WHITFIELD, A.K., LENANTON, R.C.J. 1990. Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa. *Environmental Biology of Fishes* **28**: 143-178.

RAYNIE, R.C., SHAW, R.F. 1994. Ichthyoplankton abundance a recruitment corridor from offshore spawning to estuarine nursery ground. *Estuarine, Coastal and Shelf Science* **39**: 421-450.

ROBERTS, M.J. 1990. Dispersion of a buoyant effluent discharged into the nearshore waters of Algoa Bay. M.Sc thesis 287 pp.

ROBERTS, M.J., VAN DEN BERG, M. 2005. Currents along the Tsitsikamma coast, South Africa, and potential transport of squid paralarvae and ichthyoplankton. *African Journal of Marine Science* **27**: 375-388.

SABATÉS, A., OLIVAR, M.P., SALAT, J., PALOMERA, I., ALEMANY, F. 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography* **74**: 355-376.

SENTA, T., KINOSHITA, I. 1985. Larval and juvenile fishes occurring in surf zones of western Japan. *Transactions of the American Fisheries Society* **114**: 609-618.

SHELTON, P.A. 1984. Notes on the spawning of anchovy during the summer of 1982-83. *South African Journal of Science* **80**: 69-71.

SHELTON, P.A., HUTCHINGS, L. 1981. A note on the diurnal spawning rhythm in the anchovy *Engraulis capensis* Gilchrist. *Fishery Bulletin of South Africa* **14**: 47-50.

SHELTON, P.A., HUTCHINGS, L. 1982. Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. *Journal du Conseil international pour l'Exploration de la Mer* **40**: 185-198.

SPONAUGLE, S., COWEN, R.K., SHANKS, A., MORGAN, S., LEIS, J.M., PINEDA, J., BOEHLERT, G.W., KINGSFORD, M.J., LINDEMAN, K., GRIMES, C., MUNRO, J.L. 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bulletin of Marine Science* **70**: 341-375.

STOBUTZKI, I.C. 2001. Marine reserves and the complexity of larval dispersal. *Rev Fish Biol Fish* **10**: 515-518.

STRYDOM, N.A. 2003. Occurrence of larval and early juvenile fishes in the surf zone adjacent to two intermittently open estuaries, South Africa. *Environmental Biology of Fishes* **66**: 349-359.

STRYDOM, N.A. 2007. Jetski-based plankton towing as a new method of sampling larval fishes in shallow marine habitats. *Environmental Biology of Fishes* **78**: 299-306.

STRYDOM, N.A., D'HOTMAN, B.D. 2005. Estuary-dependence of larval fishes in a non-estuary associated South African surf zone: evidence for continuity of surf assemblages. *Estuarine, Coastal and Shelf Science* **63**: 101-108.

STRYDOM, N.A., WHITFIELD, A.K., WOOLDRIDGE, T.H. 2003. The role of estuarine type in characterizing early stage fish assemblages in warm temperature estuaries, South Africa. *African Zoology* **38**: 29-43.

THOMPSON, E.F., STRYDOM, N.A., HECHT, T. 2007. Larval development of *Dagetichthys marginatus* (Soleidae) obtained from hormone-induced spawning under artificial rearing conditions. *Sciencia Marina* **71**: 421-428.

TILNEY, R.L., BUXTON, C.D. 1994. A preliminary ichthyoplankton survey of the Tsitsikamma National Park. *South African Journal of Zoology* **29**: 204-211.

TILNEY, R.L., NELSON, G., RADLOFF, S.E., BUXTON, C.D. 1996. Ichthyoplankton distribution and dispersal in the Tsitsikamma National Park marine reserve, South Africa. *South African Journal of Marine Science* **17**: 1-14.

TRICKLEBANK, K.A., JACOBY, C.A., MONTGOMERY, J.C. 1992. Composition, distribution and abundance of neustonic ichthyoplankton off northeastern New Zealand. *Estuarine, Coastal and Shelf Science* **34**: 263-275.

WATT-PRINGLE, P., STRYDOM, N.A. 2003. Habitat use by larval fishes in a temperate South African surf zone. *Estuarine Coastal and Shelf Science* **58**: 765-774.

WHITFIELD, A.K. 1989a. Ichthyoplankton in a southern African surf zone: Nursery area for the postlarvae of estuarine associated fish species? *Estuarine, Coastal and Shelf Science* **29**: 533-547.

WHITFIELD, A.K. 1989b. Ichthyoplankton interchange in the mouth region of a southern African estuary. *Marine Ecology Progress Series* **54**: 25-33.

WHITFIELD, A.K. 1998. Biology and ecology of fishes in South African Estuaries. Ichthyological Monographs of the JLB Smith Institute for Ichthyology, No. **2**: Grahamstown 232 pp.

WOOD, A.D. 2000. The description of *Austroglossus pectoralis* (Teleostei: Soleidae) larvae from the South-east coast of South Africa. *Sciencia Marina* **64**: 387-392.

WOOD, A.D. 2003. Description of larval *Cynoglossus zanzibarensis* (Teleostei: Cynoglossidae) from the Tsitsikamma Coast, South Africa. *African Journal of Marine Science* **25**: 177-183.

CHAPTER 2

COMPOSITION, ABUNDANCE, DISTRIBUTION AND SEASONALITY OF LARVAL FISHES IN THE SHALLOW NEARSHORE OF THE PROPOSED GREATER ADDO MARINE RESERVE, ALGOA BAY, SOUTH AFRICA

1. SYNOPSIS

The larval fish assemblage was investigated in the shallow, nearshore region of a proposed marine protected area in eastern Algoa Bay, temperate South Africa, prior to proclamation. Sampling was conducted at six sites along two different depth contours at ~5 and ~15 m to assess shore association. Larvae were collected by means of stepped oblique bongo net tows deployed off a ski boat, twice per season for two years between 2005 and 2007. In total, 6045 larval fishes were collected representing 32 families and 78 species. The Gobiidae, Cynoglossidae, Clupeidae, Engraulidae and Sparidae were the dominant fish families. Catches varied significantly between seasons peaking in spring with a mean of ~200 larvae/100m^3. Mean overall larval density was higher along the deeper contour, at ~15 m (40 larvae/100m^3). The preflexion stage of development dominated catches at the ~5 m (80 %) and ~15 m (73 %) depth contours. Body lengths of *Argyrosomus thorpei*, *Caffrogobius gilchristi*, *Diplodus capensis*, *Heteromycteris capensis* and *Solea turbynei*, all estuary associated species, were larger at the shallow sites nearer shore. Larvae of coastal species that produce benthic eggs dominated catches (75 %) in the shallow sites (~5 m) but were less abundant (32 %) further from shore at the deeper (~15 m) sites. All developmental stages of *Diplodus capensis*, *Engraulis capensis*, *Heteromycteris capensis*, *Sardinops sagax* and two *Pomadasys* species were found in the study area. It appears that some species use the shallow nearshore as a nursery area.

2. INTRODUCTION

Marine research in the shallow nearshore along the South African coast is limited and the use of this habitat by larval fishes is poorly understood. Many marine fish species will spawn in or near coastal habitats such as bays and estuaries to provide the early life stages with a favourable habitat for development (Potter et al., 1990; Chute and Turner, 2001; Strydom et al., 2003). Coastal habitats such as estuaries (Elliott et al., 1990; Whitfield, 1998; Strydom et al., 2003) and surf zones (Senta and Kinoshita, 1985; Boehlert and Mundy, 1988; Whitfield, 1989; Doherty and McIlwain, 1996) are well known to be important nursery areas for both larval and juvenile stages of marine species. In South Africa, temperate surf zones less than 2 m deep are dominated by the postflexion stages of marine fishes that utilize estuaries as nurseries (Strydom, 2003; Strydom and d'Hotman, 2005). These larvae are derived from marine spawned eggs that emanate from both inshore and offshore spawning grounds (Whitfield, 1989; Harris and Cyrus, 1996; Strydom, 2003). Despite the fairly well studied estuaries and surf zones of temperate South Africa, few nearshore studies exist to understand the links between offshore spawning and coastal nurseries. To date, only two nearshore larval fish studies have been conducted in the subtropical waters of KwaZulu-Natal (Harris and Cyrus, 1996; Harris et al., 1999) and three studies in the warm temperate waters of the Eastern Cape (Beckley, 1986; Tilney and Buxton, 1994; Strydom, 2007).

The close proximity of the slope waters to the continental shelf and the major influence of the Agulhas Current on the nearshore, largely determines the composition of larval fishes within the nearshore waters of subtropical KwaZulu-Natal (Harris et al., 1999). Mesopelagic and shelf species that spawn at sea and are completely independent of estuaries, including myctophids and tripterygiids, dominate nearshore ichthyoplankton catches in this region (Harris et al., 1999). Further south however, in the warm temperate Eastern Cape, the Agulhas Current is not a driving force, as the continental shelf widens considerably south of the Fish River (33°29’53’’S, 27°08’00’’E) and the current diverges from the coastline. Past studies indicated that larvae of pelagic and inshore reef fish dominate nearshore catches in this region (Beckley, 1986; Tilney and Buxton, 1994). The proximity of reefs, and other coastal nurseries such as estuaries, can also influence the composition of nearshore larval fish assemblages along the Eastern Cape coast (Beckley, 1986; Tilney and Buxton, 1994).

International research on the composition of larval fishes in the shallow nearshore is similarly lacking. In the shallow (~10 m) nearshore waters off North Western Iberia (NE Atlantic), larval fish assemblages are regulated by both abiotic and biotic characteristics (Azeiteiro et al., 2006). Other studies beyond the 15 m depth contour in nearshore coastal waters highlight the complex composition and distribution patterns of larval assemblages (Young et al., 1986; Kingsford and Choat, 1989; Gray, 1996). Not only does oceanography play a major role in determining larval fish assemblages but the spawning mode of adults, the duration of the pelagic larval stage and larval behaviour contribute significantly to the spatial and temporal patterns of nearshore larval fish assemblages (Leis, 1991). It is highly likely that with more research in South Africa, a similar pattern will emerge where nearshore assemblages of larval fishes are driven by a suite of local environmental and biological factors.

Worldwide, fish stocks are on the decline from overfishing (Svedäng and Bardon, 2003; Myers and Worm, 2003; Lotze, 2007). Marine Protected Areas (MPAs) serve as a vital tool for the management and conservation of fish populations by allowing depleted stocks to recover and furthermore by providing adjacent fished areas with larval recruits (Jennings, 2000; Leis, 2003). A new MPA is proposed for the eastern sector of Algoa Bay. No previous research has been conducted on larval fishes in this area of the bay. Studying shallow nearshore larval fish dynamics is the first step required to link this habitat to coastal nursery areas, particularly estuaries and surf zones.

The purpose of this part of the study was two-fold. Firstly to assess the composition, abundance, distribution, seasonality and developmental stages of larval fishes within the shallow nearshore zone of the proposed MPA. Secondly, to assess the occurrence of larvae along two different depth contours adjacent to the surf zone, namely ~5 and ~15 m. This work will provide more information on temporal and spatial variation in larval fish occurrence in shallow water within the proposed MPA and provide a comparative base for research once the reserve is promulgated and adult populations are re-established.

3. MATERIALS AND METHODS

3.1 Study site

Algoa Bay (Fig. 2.1), on the south east coast of South Africa, is a wide (~80 km), eastward-facing bay with depths not exceeding 70 meters (Harris, 1978). The climate of this region is classified as warm-temperate with peaks in rainfall occurring in autumn and spring (Whitfield, 1998). The Agulhas Current flows along the edge of the continental shelf in a south-westward direction approximately 80 kms offshore of

Algoa Bay (Lutjeharms, 1981). Occasionally, subtropical waters from the current will enter the bay (Schumann, 1987). South-westerly winds dominate across the bay throughout the year with the frequency of easterly winds increasing in summer (Schumann and Martin, 1991). These easterly winds are responsible for upwelling which occurs at Cape Recife to the west, with this colder water (by about 8 °C) subsequently moving westwards (Schumann et al., 1988). Westerly winds can however bring this colder upwelled water into the bay (Goschen and Schumann, 1995). Upwelling is further generated in the bottom boundary layer of the Agulhas Current at Cape Padrone in the east, with cold water penetrating into Algoa Bay (Schumann et al., 1988). Temperatures in the bay range between ~11 °C in winter to ~27 °C in summer (Beckley, 1983a; Beckley, 1988). Intense thermoclines are established in summer in the deeper sections of the bay with isothermal conditions occurring in winter. Salinity within the bay is stable, with an average of about 35.2, as freshwater inflow from rivers is limited (Schumann, 1998; Schumann et al., 2005).

Larval fishes were sampled at six sites within the proposed Greater Addo Marine Reserve between Woody Cape (33°46’71’’S, 26°20’28’’E) and Sundays Estuary (33°44’21’’S, 25°51’56”E) in the eastern sector of the bay (Fig. 2.1). Three sites were situated on the ~15 m depth contour and three sites behind the surf backline at a depth of ~5 m. For the purposes of this study, sites on the ~5 m depth contour will be defined as shallow and sites along the ~15 m depth contour will be defined as deep.

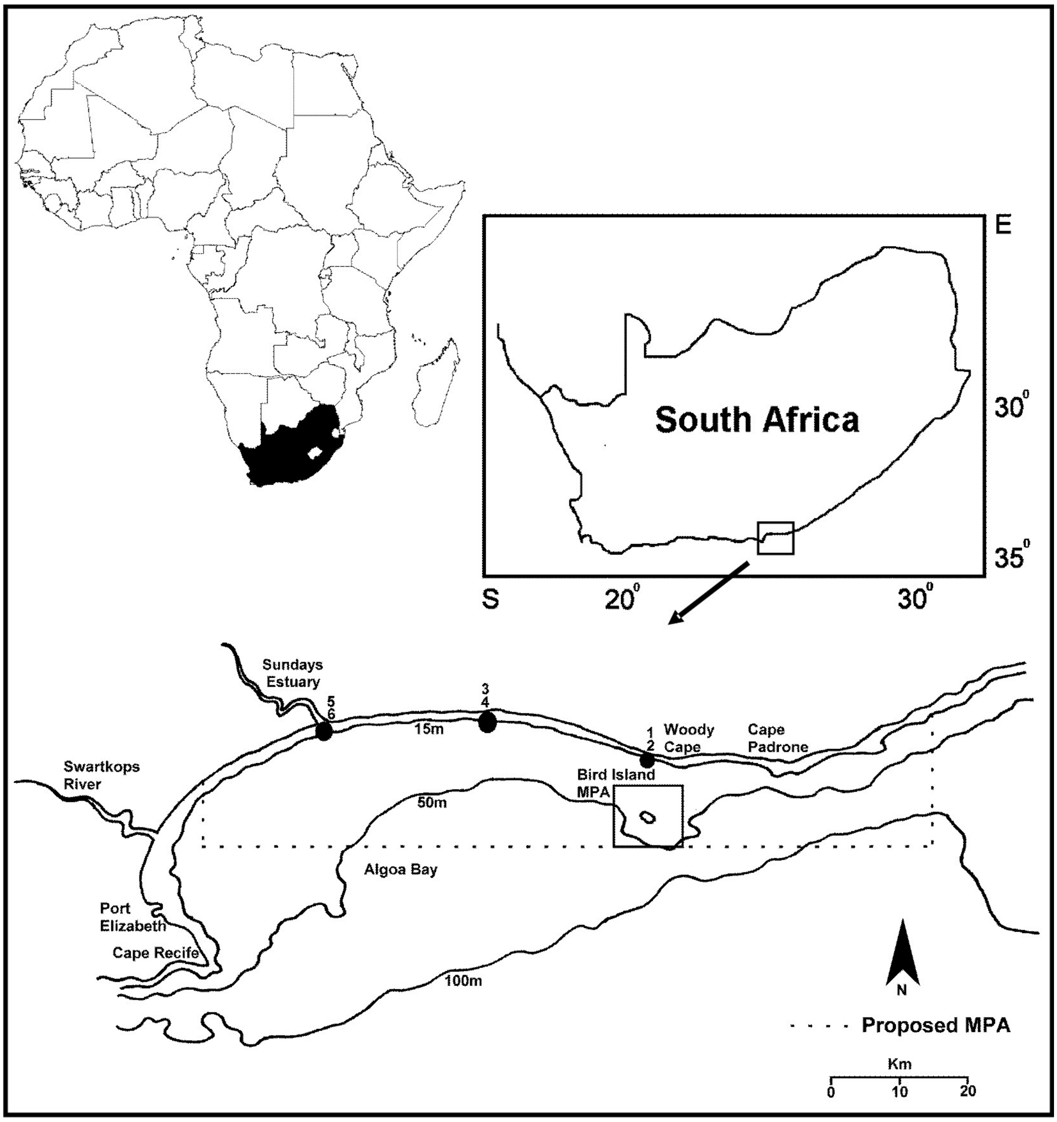

Figure 2.1: The geographical position of Algoa Bay, on the south east coast of South Africa, showing the location of the six sampling sites

3.2 Field sampling and larval identification

Collection of larval fishes took place by sampling two consecutive months per season (March and April are autumn months, June and July are winter months, September and October are spring months, December and January are summer months), for a period of two years. Consecutive months represent replicates in a season. Discrete seasonal sampling was conducted in order to assess seasonal trends occurring in the ichthyoplankton. The seasonal sampling protocol adopted in the present study is observed in similar studies (Schafer et al., 2002; Mercado et al., 2007). In total, 16 sampling trips took place between March 2005 and January 2007. At each site, larvae were collected by means of ski-boat based plankton tows using a set of bongo nets.

Each net was 3.5 m long, with a mouth diameter of 0.75 m, and a mesh aperture size of 500 µm. A General Oceanics flowmeter was suspended from the frame across the mouth of each net to quantify the volume of water sampled. The mean (± standard deviation) volume sampled by each net in this study was 170 (± 43) m^3/tow. The bongo nets were pulled parallel to the shore using a stepped oblique tow at a speed of ~2 knots. Bottom, mid and subsurface waters were sampled for 2 mins each and excluded hauling. Each tow lasted ~8 mins. Biological samples were fixed on site in 10 % formalin in seawater. Temperature, salinity and turbidity were measured at each site using a YSI 6600 multi-parameter meter. Recordings were made at the surface, middle and 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; Olivar and Fortuño, 1991; Leis, 1991; Smith and Heemstra, 1995; Neira et al., 1998; Leis and Carson-Ewart, 2000; Richards, 2005). Larvae that were positively identified in this study were grouped into estuary associated categories (Whitfield, 1998) in order to assess similarity of catch to estuaries and surf zone assemblages. 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 (Table 2.1). All larval fish terminology follows that described in Niera et al. (1998). "Larva" is a term used to describe all the stages in the early life history from hatching to attainment of a full fin ray complement, squamation, and the consequent loss of all larval characteristics (Neira et al., 1998). It is at this stage that the larva becomes a juvenile. Early juveniles were included in the study if caught. The "larva" was further divided into yolk-sac, preflexion, flexion and postflexion stages. Notochord length in preflexion and flexion larvae and standard length in postflexion larvae and early juveniles were measured to the nearest 0.1 mm and were referred to as body length (BL) in this work. The remaining zooplankton in each sample was placed into a measuring cylinder and allowed to settle for 15 – 20 minutes and a settled volume estimate of zooplankton was recorded in millilitres.

Density of larval fishes, and similarly zooplankton, was calculated using the formula:

$$\text{Density} = \frac{\text{No. of larvae or mL of zooplankton per haul}}{(\text{flow meter revolutions} \div \text{calibration value in m}^3)} \times 100$$

Table 2.1: Categories of fishes that utilise southern African estuaries (Whitfield, 1998)

Categories	Description of categories
Ib	Estuarine species that breed only in estuaries
Ib	Estuarine species that breed in estuaries and the marine environment
IIa	Euryhaline marine species that usually breed at sea, but the juveniles are dependent on estuaries as nursery areas
IIb	Euryhaline marine species that usually breed at sea, with the juveniles occurring in estuaries but also being found at sea
IIc	Euryhaline marine species that usually breed at sea, with the juveniles occurring in estuaries but being more abundant at sea
III	Marine stragglers not dependent on estuaries
IV	Freshwater species
V	Catadromous species

3.3 Data analyses

3.3.1 Environmental variability

Physical and biological data were tested for normality and homogeneity of variance using a normal probability plot, Shapiro-Wilk test and Levene's test using the STATISTICA software package version, 7.1, 2005. Appropriate transformations (square-root and log) were also used. Data did not conform to parametric test assumptions and non-parametric tests were used.

3.3.2 Seasonal trends in fish density and diversity

A Kruskal-Wallis test was used to assess differences in physical and biological data between seasons. Diversity indices (Margalef's species richness and Shannon-Wiener diversity) were calculated to one decimal point using the PRIMER statistical software package (Clarke and Warwick, 1994), and compared separately between seasons.

3.3.3 Spatial trends in fish density and diversity

Differences in temperature, salinity, turbidity, plankton and larval fish density between depth contours in the nearshore (~5 m vs. ~15 m) were assessed using a Mann-Whitney U-test. A Kruskal-Wallis test was used to assess differences in physical and biological data between sampling sites alongshore within the study area. Diversity indices (Margalef's species richness and Shannon-Wiener diversity) were calculated to one decimal point using the PRIMER statistical software package (Clarke and Warwick, 1994), and compared separately between the two different depth contours in the study area.

3.3.4 Body Length

In South Africa, larvae tend to be larger in the surf zone than in the adjacent shallow nearshore (Harris et al., 2001; Strydom, 2007). A one-tailed t-test was used to determine whether the mean body lengths of dominant ($n > 30$) larvae at the ~5 m depth contour were significantly larger than mean body lengths of dominant ($n > 30$) larvae at the ~15 m depth contour. Length data were tested for normality and homogeneity of variance using a normal probability plot, Shapiro-Wilk test and Levene's test using the STATISTICA software package version, 7.1, 2005.

3.3.5 Environmental correlation and community analysis

Patterns between environmental variables and larval fish densities were examined with Principal Component Analysis using the PRIMER statistical software package (Clarke and Warwick, 1994). Physical and biological data were log transformed ($\log(x+0.1)$) to remove bias from fish larvae of a few species with high densities. Eigenvalues and eigenvectors were extracted from a correlation matrix. Spearman's rank order correlation was used to determine whether physical variables displayed any significant relationship with fish density. Community analysis was conduced using the PRIMER statistical software package (Clarke and Warwick, 1994). Species data were square-root transformed or transformed based on species presence or absence prior to analysis and a Bray-Curtis similarity matrix was generated for seasons, depth contours and stations alongshore (i.e. between Woody Cape and Sundays River). Clusters in a dendrogram format were assessed using group average hierarchical sorting, and ANOSIM was used to detect differences between groups in each analysis. The SIMPER routine was applied to determine the relative contribution of key species to the similarity or difference between seasons, depth contours and stations alongshore.

4. RESULTS

4.1 Environmental variability

A significant difference in temperature ($H = 64.2$; $n = 96$; $P = 0.0001$), salinity ($H = 21.2$; $n = 96$; $P = 0.0001$) and turbidity ($H = 9.5$; $n = 96$; $P = 0.023$) occurred between the seasons during the study period (Fig. 2.2). Mean water temperature ranged from 21.6 °C in summer to 15.8 °C in winter. Mean salinity ranged from 35.6 in autumn to 33.9 in winter and mean turbidity ranged from 22.9 NTU in spring to 0.7 NTU in summer. Similarly, mean zooplankton density fluctuated significantly ($H = 12.2$; $n =$

96; P = 0.006) between seasons (Fig. 2.2) peaking in autumn (1469.0 mL/100m^3) and decreasing in summer (24.0 mL/100m^3).

No significant difference in temperature, salinity, turbidity or zooplankton density was observed alongshore, i.e. between Woody Cape and the Sundays Estuary. Similarly, no significant difference in these environmental variables or zooplankton density was observed between the ~5 m and ~15 m depth contours.

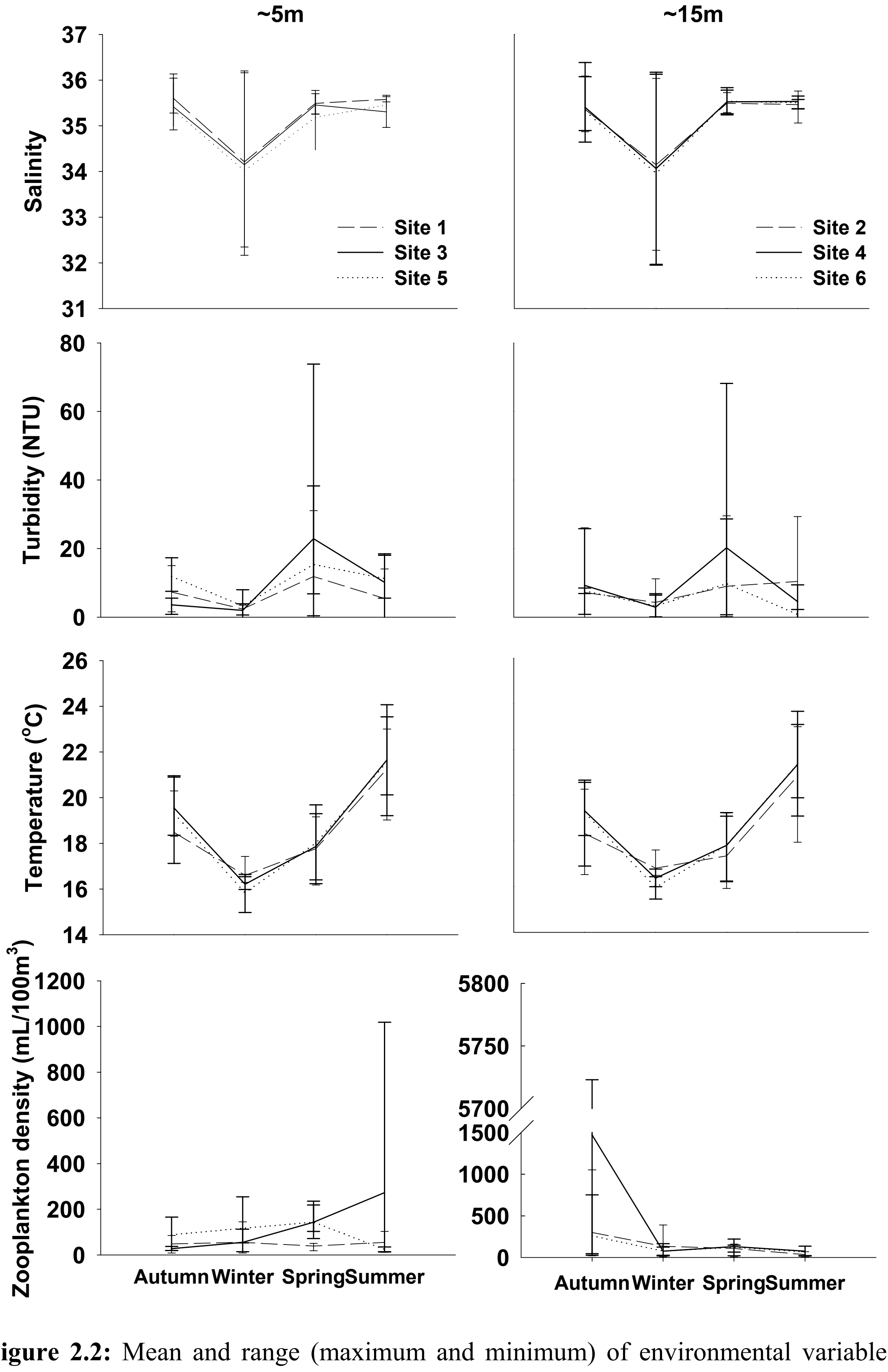

Figure 2.2: Mean and range (maximum and minimum) of environmental variables and zooplankton density recorded seasonally at each site alongshore i.e. between Woody Cape and the Sundays Estuary and at the two depth contours (i.e. ~5 and ~15 m) within the shallow nearshore during the study (2005 – 2007). Values include all samples in a given season over both years for each sampling depth contour (n = 4)

4.2 Species composition and estuary association

A total of 6045 larval fishes were caught, comprising 32 fish families and 78 species (Table 2.2). The study area was dominated by the larvae of 10 fish families. The Gobiidae was the dominant family and made a 49 % contribution to the total catch. The Cynoglossidae, Engraulidae and Clupeidae each contributed 8 % to the total catch. The Sparidae contributed 7 % to the total catch. The Blenniidae and Soleidae contributed 5 % and 4 % to the total catch respectively. Sciaenidae contributed 3 % to the catch while the Tripterygiidae and Kyphosidae contributed 2 % and 1 % respectively. All other fish family contributions were each less than 1 % to the catch.

Marine species (category III), not dependent on estuaries, dominated the nearshore larval fish assemblage (37 %) during the study period (Table 2.2). Estuary-resident species (category I) (10 %) and estuary associated marine species (category II) (7 %) made smaller contributions to the overall larval fish catch. Only one catadromous species, *Myxus capensis*, was encountered during the study period. Unidentified species contributed 46 % towards the catch.

4.3 Seasonal trends in fish density and diversity

The density of larval fishes varied significantly ($H = 5.2$, $n = 96$ $P = 0.04$) between seasons (Fig. 2.3). The highest mean density of larval fishes was recorded in spring (199 larvae/100m^3) and ranged from 1 to 717 larvae/100m^3. Lowest mean density (7 larvae/100m^3) occurred in summer and ranged from 4 to 76 larvae/100m^3. Mean density varied little between autumn (29 larvae/100m^3 and ranged from 1 to 267 larvae/100 m^3) and winter (25 larvae/100m^3 and ranged from 1 to 128 larvae/100 m^3).

The dominant species (> 1%) including *Argyrosomus thorpei*, *Cremnochorites capensis*, *Cynoglossus capensis*, *Engraulis capensis*, Gobiid 3, Gobiid 4, *Heteromycteris capensis*, *Sardinops sagax*, *Solea turbynei*, Sparid 1 and *Spondyliosoma emarginatum* all showed peaks in density during spring or summer (Table 2.2). There were however dominant species including Blenniid 4, *Diplodus capensis* and Kyphosid 1 where peaks in density were observed during winter.

Table 2.2: Species composition, mean density (range) at each depth contour (~5 vs. ~15 m), total catch, mean body length (range), developmental stage, estuary association and season of greatest density of larval fishes caught in the shallow nearshore of Algoa Bay. Pr = preflexion, F = flexion, Po = postflexion, Ej = early juvenile. Dominant developmental stages bolded

Family	**Species**	**Mean Density (Range) (No/100m^3)**		**Total Catch**		**Mean Body Length (Range) (mm)**	**Developmental Stage**	**Estuary association**	**Season**
		~5 m	**~15 m**	**No.**	**%**				
Atherinidae	Atherinid 1	0.01 (0 – 0.7)	0	1	<1	7.9	**F**	?	Summer
Blenniidae	Blenniid 1	0.1 (0 – 4.5)	0.01 (0 – 0.6)	15	<1	2.5 (2.3 – 2.9)	**Pr**, F	?	Summer
	Blenniid 2	0.2 (0 – 1.9)	0.1 (0 – 1.8)	33	<1	2.9 (1.4 – 8.0)	**Pr**, F	?	Spring
	Blenniid 3	0.09 (0 – 1.3)	0.05 (0 – 0.7)	12	<1	2.6 (1.6 – 6.3)	**Pr**, F	?	Winter
	Blenniid 4	1.2 (0 – 39.4)	0.8 (0 – 8.1)	146	2.4	6.1 (3.2 – 13.5)	Pr, **F**, Po	?	Winter
	Omobranchus woodi	0.3 (0 – 8.7)	0.1 (0 – 1.3)	43	<1	4.1 (2.3 – 7.4)	**Pr**, F	Ia	Summer
	Parablennius pilicornis	0.06 (0 – 0.7)	0.2 (0 – 2.1)	28	<1	3.3 (2.4 – 7.9)	**Pr**, F	III	Summer
Callionymidae	*Callionymis marlyi*	0.04 (0 – 0.7)	0.04 (0 – 0.8)	6	<1	2.4 (1.6 – 3.1)	**Pr**	III	Winter
Carangidae	Carangid 1	0	0.05 (0 – 2.5)	4	<1	3.0 (2.5 – 3.6)	**Pr**	III?	Summer
	Trachurus capensis	0	0.01 (0 – 0.8)	1	<1	4.2	**Pr**	III	Winter
Cheilodactylidae	Cheilodactylid 1	0.06 (0 -1.2)	0.09 (0 – 2.7)	12	<1	2.9 (2.3 – 3.4)	**Pr**	III?	Winter
Clinidae	*Clinus superciliousus*	0.02 (0 – 0.5)	0.01 (0 – 0.4)	3	<1	10.6 (8.5 – 14.4)	**Po**	Ib	Winter
Clupeidae	*Etrumeus whiteheadi*	0.1 (0 -2.7)	0.1 (0 – 3.0)	19	<1	10.6 (5.6 – 14.6)	Pr, **F**, Po	III	Spring
	Sardinops sagax	0.6 (0 – 8.0)	4.7 (0 – 35.4)	451	7.4	6.2 (2.1 – 17.7)	**Pr**, F, Po	III	Summer
Cynoglossidae	*Cynoglossus capensis*	0.2 (0 – 8.4)	3.3 (0 -126.6)	281	4.6	3.1 (1.9 – 5.6)	**Pr**, F	III	Spring
	Cynoglossus zanzibarensis	0.3 (0 – 5.8)	2.5 (0 – 76.8)	229	3.7	3.8 (1.5 – 8.0)	**Pr**	III	Autumn
Engraulidae	*Engraulis capensis*	1.8 (0 – 21.8)	5.3 (0 – 82.4)	476	7.8	4.8 (2.1 – 19.5)	**Pr**, F, Po	III	Spring
Gadidae	*Gaidropsarus capensis*	0.03 (0 – 1.3)	0.1 (0 – 2.7)	12	<1	1.8 (1.2 – 2.1)	**Pr**	III	Winter
	Merluccius paradoxus	0.01 (0 – 0.6)	0	1	<1	3.0	**Pr**	III	Winter
Gobiesocidae	*Apletodon pellagrini*	0	0.04 (0 – 2.0)	2	<1	15.6 (11.3 – 19.8)	**Ej**	III	Autumn
	Chorisochismus dentex	0.02 (0 – 0.5)	0.01 (0 -0.6)	3	<1	3.9 (2.9 – 4.7)	**Pr**	III	Winter
	Diplogaster megalops	0.05 (0 -1.2)	0.5 (0 – 5.8)	36	<1	3.1 (2.0 – 5.3)	**Pr**, F	III	Spring
	Eckloniaichtys scylliorhiniceps	0.04 (0 – 0.9)	0.1 (0 – 6.8)	18	<1	3.7 (2.0 – 5.4)	**Pr**, F, Po	III	Spring
	Lepadicthys sp 1	0.009 (0 – 0.4)	0	1	<1	3.2	**Pr**	III?	Winter
Gobiidae	*Caffrogobius gilchristi*	0.3 (0 – 5.1)	0.7 (0 – 11.5)	87	1.4	2.7 (1.5 – 4.5)	**Pr**, F	Ib	Autumn
	Caffrogobius nudiceps	2.0 (0 – 83.8)	3.3 (0 -57.6)	436	7.2	3.3 (1.6 – 6.2)	**Pr**, F, Po	Ib	Autumn
	Caffrogobius species 1	0.008 (0 – 0.4)	0.05 (0 – 1.9)	3	<1	2.6 (2.0 – 2.9)	**Pr**	Ib?	Autumn
	Gobiid 1	0.3 (0 – 7.2)	0.2 (0 – 9.6)	34	<1	2.9 (2.0 – 4.6)	**Pr**, F	?	Autumn

Family	**Species**	**Mean Density (Range) (No/100m³)**		**Total Catch**		**Mean Body Length (Range) (mm)**	**Developmental Stage**	**Estuary association**	**Season**
		~5 m	**~15 m**	**No.**	**%**				
	Gobiid 2	1.2 (0 – 22.2)	2.9 (0 – 107.7)	320	5.2	3.6 (1.9 – 8.1)	**Pr**, F, Po	?	Autumn
	Gobiid 3	1.9 (0 – 51.1)	1.8 (0 – 47.9)	341	5.6	3.8 (2.2 – 8.6)	**Pr**, F, Po	?	Spring
	Gobiid 4	13.9 (0 – 650.0)	1.1 (0 – 29.0)	1745	28.8	7.1 (3.0 – 16.0)	Pr, F, **Po**	?	Spring
	Psammogobius knysnaensis	0.1 (0 -2.9)	0.04 (0 – 1.9)	11	<1	4.1 (2.2 – 6.0)	Pr, **F**	Ib	Summer
	Redigobius dewaali	0.008 (0 – 0.4)	0.01 (0 – 0.5)	2	<1	3.0 (2.6 – 3.5)	**Pr**	Ib	Summer
Haemulidae	*Pomadasys* sp 1	0.02 (0 – 0.7)	0.2 (0 – 3.7)	25	<1	5.1 (2.5 – 11.0)	**Pr**, F, Po	IIa?	Autumn
	Pomadasys sp 2	0.03 (0 – 0.6)	0.2 (0 – 4.2)	22	<1	3.7 (2.1 – 7.2)	**Pr**, F, Po	IIa?	Summer
Kyphosidae	Kyphosid 1	0.2 (0 – 8.3)	0.6 (0 – 11.3)	66	1.0	2.7 (2.1 – 4.1)	**Pr**	III?	Winter
Leiognathidae	Leiognathid 1	0	0.01 (0 – 0.4)	1	<1	3.2	**F**	II?	Autumn
Lophiidae	Lophid 1	0.01 (0 – 0.5)	0	1	<1	3.1	**F**	III?	Winter
Macroramphosidae	*Macroramphosus scolopax*	0.01 (0 – 0.7)	0	1	<1	4.3	**Pr**	III	Winter
Monodactylidae	*Monodactylus falciformis*	0.1 (0 -1.4)	0.01 (0 – 0.6)	14	<1	5.0 (3.7 – 5.7)	**F**	IIa	Summer
Mullidae	Mullid 1	0.01 (0 – 0.6)	0	1	<1	4.0	**Pr**	III?	Autumn
	Mullid 2	0.01 (0 – 0.7)	0	1	<1	3.5	**Pr**	III?	Winter
Mugilidae	*Myxus capensis*	0.01 (0 – 0.8)	0	1	<1	5.7	**F**	V	Summer
Myctophidae	Myctophid 1	0.01 (0 – 0.7)	0	1	<1	3.8	**Pr**	III?	Winter
Nomeidae	Nomeid 1	0.02 (0 – 1.0)	0.03 (0 – 1.2)	5	<1	2.0 (1.9 – 2.2)	**Pr**	III?	Autumn
Scaridae	Scarid 1	0.01 (0 – 0.8)	0.01 (0 – 0.8)	3	<1	8.2 (8 – 8.7)	**Po**	III?	Winter
Sciaenidae	*Argyrosomus japonicus*	0.3 (0 – 7.6)	0.3 (0 – 8.6)	56	<1	4.1 (1.8 – 6.0)	**Pr**, F	IIa	Spring
	Argyrosomus thorpei	0.4 (0 – 6.0)	1.3 (0 -26.8)	147	2.4	2.3 (1.2 – 8.4)	**Pr**, F	III	Spring
	Umbrina canariensis	0	0.08 (0 – 1.7)	7	<1	3.8 (2.8 – 5.4)	**Pr, F**	III	Summer
Scorpaenidae	Scorpaenid 1	0.04 (0 – 2.2)	0.2 (0 – 8.4)	22	<1	2.6 (1.8 – 3.5)	**Pr**	III?	Spring
Sillaginidae	*Sillago silhama*	0.04 (0 – 0.7)	0.01 (0 – 0.5)	4	<1	4.3 (2.7 – 5.8)	**Pr**, F	IIc	Winter
Soleidae	*Heteromycteris capensis*	0.3 (0 – 7.2)	1.6 (0 – 38.1)	153	2.5	2.9 (1.2 – 7.8)	**Pr**, F, Po	IIb	Spring
	Solea fulvomarginatum	0.02 (0 – 0.5)	0.02 (0 – 0.5)	4	<1	3.6 (3.2 – 4.0)	**Pr**, **F**	III	Spring
	Solea turbynei	0.6 (0 – 8.7)	0.4 (0 – 3.6)	97	1.6	3.4 (1.2 – 4.5)	Pr, **F**, Po	IIb	Summer
Sparidae	*Acanthopagrus berda*	0.08 (0 – 0.7)	0.1 (0 – 2.1)	16	<1	4.3 (3.2 – 6.3)	**Pr**, F	IIa	Winter
	Diplodus capensis	0.3 (0 – 2.7)	0.5 (0 – 10.0)	75	1.2	5.4 (2.5 – 9.9)	Pr, **F**, Po	IIc	Winter
	Diplodus cervinus	0.03 (0 – 0.6)	0.04 (0 – 1.3)	6	<1	5.4 (2.3 – 7.6)	**Pr**, F, **Po**	III	Winter
	Gymnocrotaphus curvidens	0.01 (0 – 0.5)	0	1	<1	5.5	**F**	III	Winter
	Pachymetopon aeneum	0	0.07 (0 – 0.6)	6	<1	4.4 (3.0 – 5.2)	**Pr**, F	III	Winter
Sparidae	*Pagellus natalensis*	0	0.02 (0 – 1.2)	2	<1	4.4 (4.0 – 4.8)	**Pr**	III	Winter

Family	**Species**	**Mean Density (Range) (No/100m^3)**		**Total Catch**		**Mean Body Length (Range) (mm)**	**Developmental Stage**	**Estuary association**	**Season**
		~5 m	**~15 m**	**No.**	**%**				
	Rhabdosargus holubi	0.02 (0 – 0.7)	0	2	<1	9.1 (8.6 – 9.5)	**F**, **Po**	IIa	Spring
	Rhabdosargus sarba	0.02 (0 – 1.0)	0.1 (0 – 4.4)	5	<1	7.7 (6.5 – 9.0)	**F**	IIb	Summer
	Sparid 1	0.3 (0 – 7.0)	0.9 (0 -14.8)	97	1.6	2.7 (1.4 – 4.0)	**Pr**, F	?	Spring
	Sparid 2	0	0.02 (0 – 0.8)	2	<1	4.4 (4.3 – 4.5)	**Pr**	?	Winter
	Sparid 3	0.03 (0 – 0.7)	0.04 (0 – 0.7)	6	<1	4.6 (3.8 – 5.1)	Pr, **F**	?	Winter
	Sparid 4	0	0.02 (0 – 0.5)	2	<1	4.7 (4.6 – 4.8)	**F**	?	Winter
	Spondyliosoma emarginatum	0.1 (0 – 2.1)	2.3 (0 – 25.3)	223	3.6	2.7 (1.2 – 7.2)	**Pr**, F	III	Summer
Syngnathidae	*Nannocampus elegans*	0.01 (0 – 0.6)	0	1	<1	19.2	**Po**	III	Autumn
	Sygnathus acus	0.02 (0 – 0.7)	0	3	<1	16.3 (15.2 – 17.3)	**Po**	Ib	Autumn
Tetradontidae	Tetradontid 1	0.08 (0 – 0.6)	0.02 (0 – 0.5)	11	<1	4.1 (2.2 – 8.6)	**Pr**, Po	III?	Spring
Trigilidae	Triglid 1	0.09 (0 – 4.1)	0.1 (0 – 5.3)	21	<1	3.0 (2.5 – 3.5)	**Pr**	III?	Winter
Tripterygiidae	*Cremnochorites capensis*	0.2 (0 – 2.2)	0.9 (0 -15.6)	103	1.7	5.7 (3.6 – 11.0)	Pr, **F**, Po	III	Summer
	Unidentified Species 1	0.02 (0 – 0.6)	0	2	<1	2.1 (2.0 – 2.2)	**Pr**	?	Autumn
	Unidentified Species 2	0.01 (0 – 0.6)	0	1	<1	1.8	**Yo**	?	Autumn
	Unidentified Species 3	0	0.02 (0 – 1.1)	1	<1	6.5	**F**	?	Autumn
	Unidentified Species 4	0	0.01 (0 – 0.8)	1	<1	9.3	**F**	?	Winter
	Unidentified Species 5	0	0.01 (0 – 0.8)	1	<1	2.7	**Pr**	?	Winter
	Unidentified Species 6	0.01 (0 – 0.8)	0.1 (0 – 5.3)	10	<1	2.3 (2.0 – 2.9)	**Pr**	?	Spring

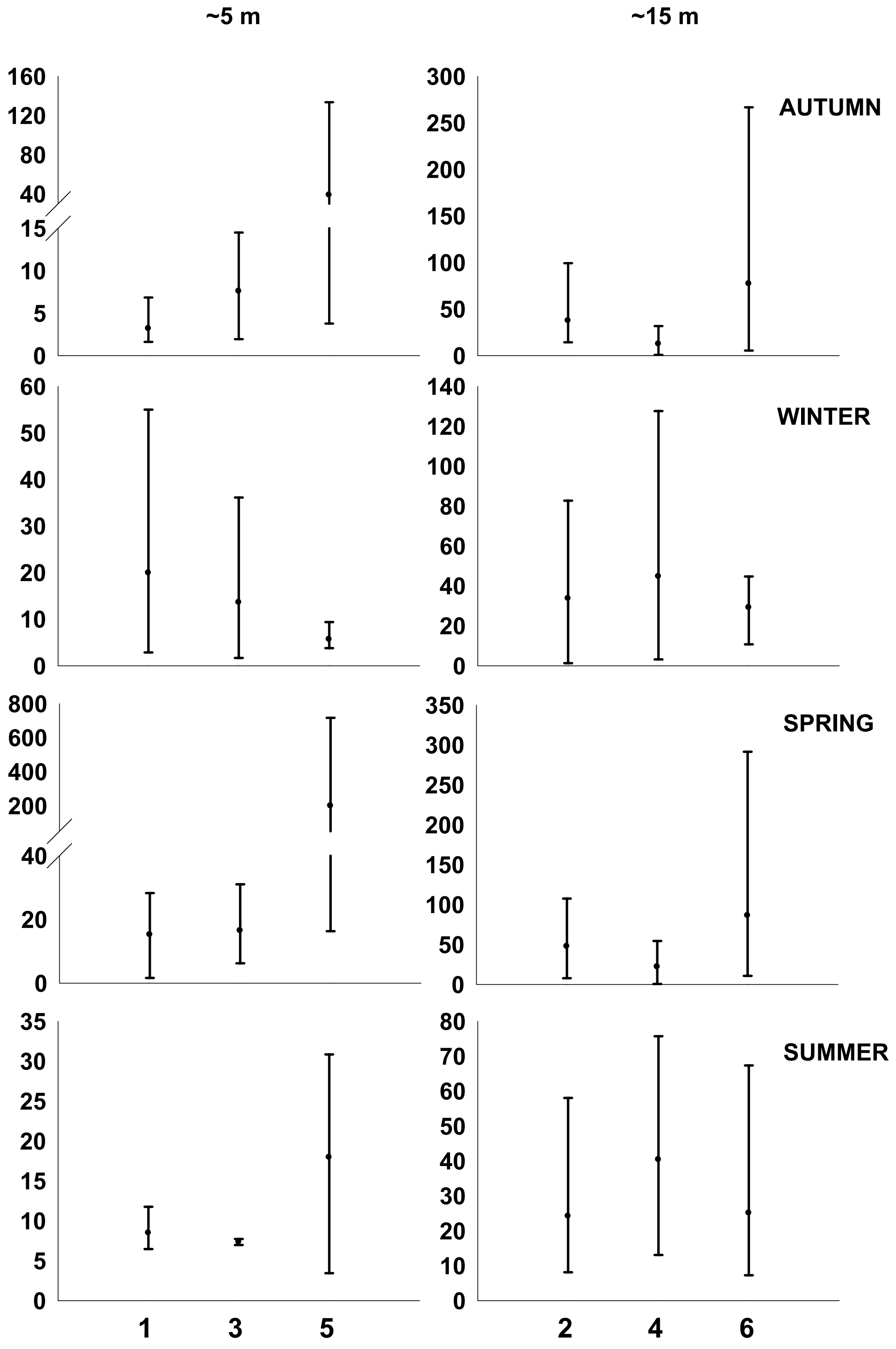

Figure 2.3: Mean and range (maximum and minimum) of larval fish density recorded seasonally at each site alongshore i.e. between Woody Cape and the Sundays Estuary and at the two depth contours (i.e. ~5 and ~15 m) within the shallow nearshore during the study (2005 – 2007). Note variable vertical scales. Values include all samples in a given season over both years for each sampling depth (n = 4)

Species richness (d) of 21.4 and species diversity (H’) of 3.0 was obtained for the eastern sector of Algoa Bay. Species diversity peaked in summer (d = 12.4, H’ = 2.9), decreased slightly in spring (d = 14.8, H’ = 2.8) and in autumn (d = 16.4, H’ = 2.5), while lowest diversity was recorded in winter (d = 10.7, H’ = 1.7).

4.4 Spatial trends in fish density and diversity

Although no significant difference in overall larval fish density occurred alongshore, i.e. between Woody Cape and the Sundays Estuary, a significant difference in the densities of some dominant species, namely *Argyrosomus thorpei* (H = 6.9; n = 96; P = 0.03), gobiid 2 (H = 7.1; n = 96; P = 0.03) and gobiid 4 (H = 11.1; n = 96; P = 0.003) occurred alongshore with greatest mean densities observed off the Sundays Estuary mouth. Similarly a significant difference (H = 6.2; n = 96; P = 0.04) in the density of *Etrumeus whiteheadi* occurred alongshore, with the highest mean density of this species recorded at the centre of the study area.

A significant difference (Z = 3.2; n = 96; P = 0.001) in overall larval fish density was observed between the two different depth contours sampled. Overall, mean larval fish densities were higher on the deeper ~15 m depth contour (40 larvae/100m^3) than the shallower contour just behind the surf zone (30 larvae/100m^3). Similarly, species diversity was greatest at the deeper sites on the ~15 m depth contour (d =16.8, H’ = 3.1) when compared to the shallower sites just behind the surf zone (d = 19.4, H’ = 2.4). Larval fish density ranged from 1 – 717 larvae/100m^3 just behind the surf zone (~5 m) and from 1 – 292 larvae/100 m^3 at the ~15m depth contour. Similarly, a significant difference in densities of *Caffrogobius nudiceps* (Z = 2.6; n = 96; P = 0.003), *Cynoglossus zanzibarensis* (Z = 2.4; n = 96; P = 0.01), *Heteromycteris capensis* (Z = 2.6; n = 96; P = 0.009), *Sardinops sagax* (Z = 3.1; n = 96; P = 0.002), sparid 1 (Z = 2.4; n = 96; P = 0.01), and *Spondyliosoma emarginatum* (Z = 2.5; n = 96; P = 0.01) occurred between the two different depth contours sampled, with mean densities greatest on the deeper (~15 m) contour.

In the present study, the number of larvae from coastal species that produce benthic eggs dominated catches (75 %) in the shallow sites. Larvae of these species were less abundant (32 %) further from shore at the deeper (~15 m) sites. Larvae of coastal species that produce pelagic eggs made a total contribution of 10 % towards larval fish catches in the shallower sites (~5 m) but in the deeper sites (~15 m) contributed 22 % to the catch. Larvae of pelagic species that produce pelagic eggs contributed just 9 % towards the catch in the shallower sites (~5 m) but contributed 26 % towards the catch in the deeper sites (~15 m). Unidentified species contributed 6 % and 20 % towards the catch in the ~5 m and ~15 m sites respectively.

4.5 Developmental stage

Preflexion larvae comprised over 75 % of the catch in the shallow nearshore. This developmental stage dominated catches across all sites and both depth contours sampled. Preflexion larvae contributed 73 % towards the total catch at the shallower sites (~5 m) and 79 % at the deeper sites (~15 m). Larvae in the flexion stage of development contributed 20 % towards the total catch in the shallower sites and 17 % in the deeper sites. Only 7 % of the total catch in the shallower sites consisted of postflexion larvae while this stage only compromised 4 % in deeper sites.

4.6 Body Length

A significant difference in the lengths of *Sardinops sagax* (P = 0.007), Goby 3 (P = 0.003) and Goby 4 (P = 0.01) occurred between the two different depth contours with a smaller mean length observed in the shallow ~5 m contour for each species (Table 2.3). Conversely estuary associated species, namely *Diplodus capensis* (P = 0.02), *Caffrogobius gilchristi* (P = 0.005), *Heteromycteris capensis* (P = 0.03) and *Solea turbynei* (P = 0.001) were significantly larger in shallower water (~5 m).

Table 2.3: Mean body lengths (range) of dominant species (n = 30) at the two different depth contours (~5 and ~15 m)

Dominant Species	**Estuary Dependence**	**n**	**~5 m mean length (range) (mm)**	**n**	**~15 m mean length (range) (mm)**	**p-value**	**t-value**
Argyrosomus thorpei	Marine	30	2.8 (1.5 – 8.4)	30	2.4 (1.5 – 4.1)	<0.05	1.7
Blenniid 4	?	30	5.8 (3.8 – 10)	30	6.6 (4.2 – 13.5)	0.1	-1.7
Caffrogobius gilchristi	Resident	30	2.9 (1.8 – 4.5)	30	2.5 (1.7 – 3.4)	<0.01	2.5
Caffrogobius nudiceps	Resident	30	3.1 (2.0 – 5.3)	30	3.3 (2.1 – 4.5)	0.3	-1.1
Cremnochorites capensis	Marine	30	6.1 (4.5 – 8.7)	30	6.0 (4.7 – 8.5)	0.8	0.2
Cynoglossus capensis	Marine	30	3.2 (2.4 – 5.4)	30	3.0 (1.9 – 5.4)	0.5	0.7
Cynoglossus zanzibarensis	Marine	30	3.3 (2.0 – 5.4)	30	3.9 (2.8 – 5.8)	0.2	-1.4
Diplodus capensis	Dependent	30	6.0 (2.5 – 9.9)	30	5.0 (3.5 – 6.6)	<0.05	2.2
Engraulis capensis	Marine	30	5.4 (3.1 – 12.7)	30	5.0 (2.6 – 8.1)	0.4	0.8
Gobiid 2	?	30	3.4 (2.3 – 5.3)	30	3.5 (1.9 – 5.9)	0.6	-0.6
Gobiid 3	?	30	3.3 (2.4 – 5.6)	30	4.1 (2.3 – 8.5)	<0.001	-3.1
Gobiid 4	?	30	6.6 (3.0 – 9.2)	30	7.6 (4.9 – 16.3)	<0.05	-1.7
Heteromycteris capensis	Dependent	30	4.6 (1.5 – 7.8)	30	2.6 (2.0 – 4.0)	<0.05	2.2
Kyphosid 1	?	30	2.8 (2.1 – 4.1)	30	2.6 (2.1 – 3.0)	0.1	1.6
Sardinops sagax	Marine	30	5.4 (3.2 – 15.0)	30	7.1 (3.8 – 14.1)	<0.001	-2.8
Solea turbynei	Dependent	30	3.8 (3.0 – 4.4)	30	3.0 (1.2 – 3.9)	<0.001	5.3
Sparid 1	?	30	2.7 (2.1 – 3.7)	30	2.6 (1.4 – 3.8)	0.4	0.8
Spondyliosoma emarginatum	Marine	30	2.9 (2.1 – 3.9)	30	2.6 (1.9 – 3.2)	0.1	0.2

4.7 Environmental correlation and community analysis

Biological data collected during the 2006 summer field survey was not included in the principal component analysis (PCA) as no corresponding environmental variables were recorded during this field survey due to technical equipment error. PCA indicated that 34 % of the variability in larval fish density could be explained by the first eigenvector (PC 1) (Table 2.4). PC 1 was characterized by a negative correlation with both temperature and salinity. The second eigenvector (PC 2) explained 26 % of the variability and was associated with a negative correlation with turbidity. These two factorial axes explained >60 % of the total variability (Fig. 2.4). The distribution of samples in the space defined by the first 2 axes yielded groupings of samples by season and demonstrates that water masses influence larval fish community structure. A group situated between 1 and 2 on the PCA y-axis and between -2 and 0 on the PCA x-axis included samples from summer, explained by higher temperatures ranging from 20.2 – 24.1 °C, higher salinities ranging between 35 – 35.8 and lower turbidity values ranging from 2.2 – 29.4 NTU. A grouping of samples between 1 – 3 on the PCA x-axis, included winter samples defined by lower temperatures ranging from 15 – 17.6 °C and lower salinities ranging from 32.0 - 35. A group of samples between 0 and 1 on the PCA x-axis included samples from spring when larval densities were greatest exceeding 700 larvae/100m^3. During this spring period temperatures were low ranging between 16 – 19 °C and turbidity was high reaching up to 74 NTU. A group of mixed samples were tightly grouped together between -1 and 0 on the PCA x-axis and between 0.5 and -1.5 on the PCA y-axis. This collection of predominately autumn samples but including a few summer, winter and spring samples were grouped together when environmental variables were stable, where temperatures ranged between 17.9 – 21 °C and salinities ranged between 35 – 35.4.

Table 2.4: Eigenvectors determined from PCA for environmental variables and total larval fish density

	Factor 1	**Factor 2**	**Factor 3**	**Factor 4**
% Variance explained	34.2	26.4	24.6	14.9
Temperature	-0.69	0.23	0.13	0.67
Salinity	-0.68	0.01	-0.35	-0.64
Turbidity	-0.07	-0.84	-0.44	0.30
Larval fish density	0.22	0.49	-0.82	0.22

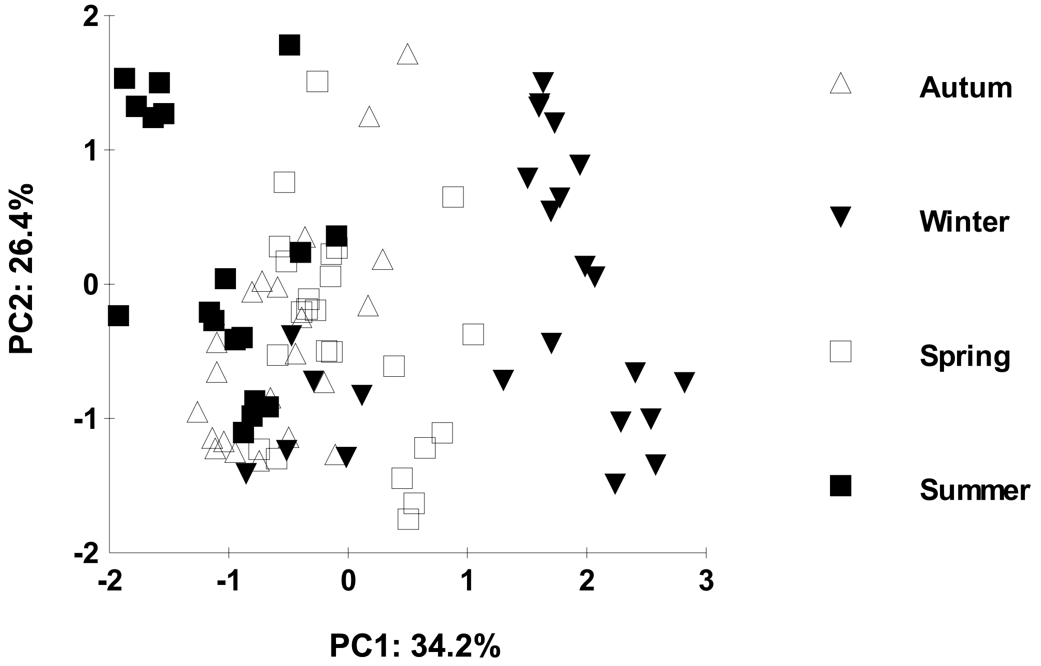

Figure 2.4: Representation of seasonal variation in the first two axes of the PCA in the shallow nearshore of Algoa Bay (2005 – 2007). Variables including temperature, salinity, turbidity and larval fish density used in PCA analysis (n = 83)

Spearman's rank order correlation indicated that zooplankton density had a significant positive relationship with total larval fish density (Table 2.5) and trends in larval fish and zooplankton densities can be observed in Figure 2.5. Zooplankton density, salinity, temperature and turbidity all had significant relationships with the densities of dominant larval fishes in the study area including *Argyrosomus thorpei*, *Caffrogobius nudiceps*, *Cynoglossus capensis*, *Heteromycteris capensis*, *Sardinops sagax* and *Solea turbynei*.

Table 2.5: Spearman rank order correlation coefficient for larval fish density versus environmental variables for all taxa and dominant species (>1 % of total catch) recorded in the shallow nearshore of the eastern sector of Algoa Bay (2005 – 2007). ns = not significant

Species	**Plankton**	**Salinity**	**Temperature**	**Turbidity**
All taxa	0.43	ns	ns	ns
Dominant species:				
Argyrosomus thorpei	ns	ns	ns	0.23
Blenniid 4	ns	-0.23	-0.26	-0.29
Caffrogobius gilchristi	ns	ns	ns	ns
Caffrogobius nudiceps	ns	-0.28	ns	ns
Cremnochorites capensis	ns	ns	ns	ns
Cynoglossus capensis	0.25	-0.30	-0.31	ns
Cynoglossus zanzibarensis	ns	ns	ns	ns
Diplodus capensis	ns	ns	ns	ns
Engraulis capensis	ns	ns	ns	ns
Gobiid 2	0.24	ns	ns	ns
Gobiid 3	0.34	-0.30	ns	ns
Gobiid 4	0.28	ns	ns	0.20
Heteromycteris capensis	0.39	ns	ns	ns
Kyphosid 1	0.26	-0.36	-0.35	ns
Sardinops sagax	ns	ns	ns	-0.26
Solea turbynei	ns	0.55	ns	ns
Sparid 1	ns	ns	ns	ns
Spondyliosoma emarginatum	ns	ns	ns	ns

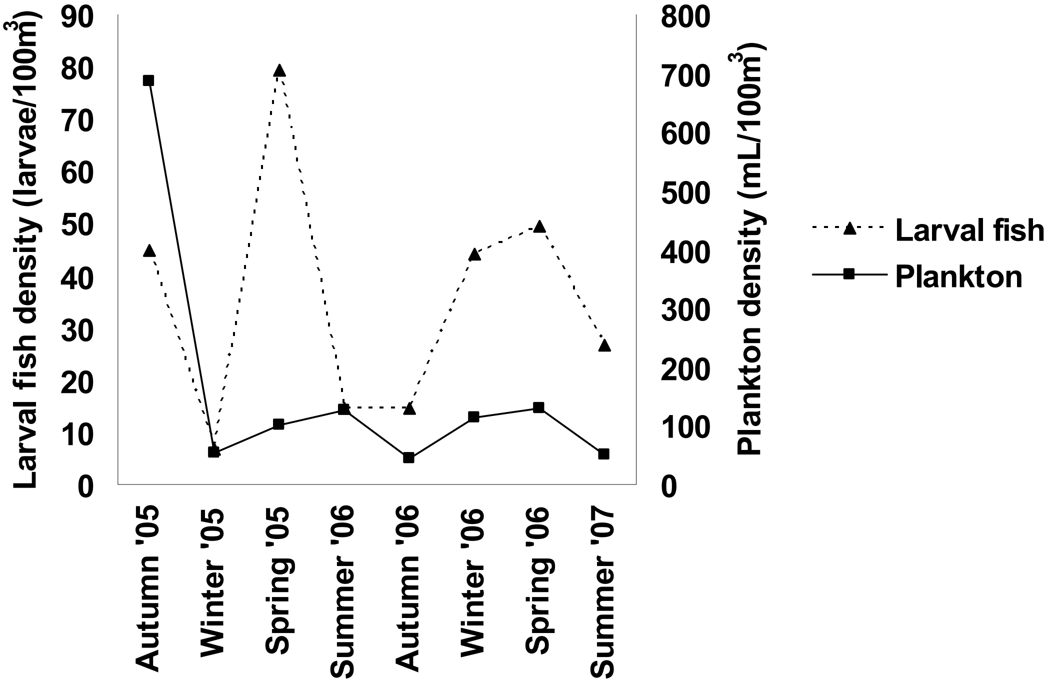

Figure 2.5: Mean seasonal changes in combined larval fish density at both depth contours and zooplankton density in the shallow nearshore of Algoa Bay (2005 – 2007)

5. DISCUSSION

5.1 Larval fish composition

Catches of larvae of coastal fishes in this study (78 species representing 32 fish families) were considerably higher than that recorded by Beckley (1986) in the shallow nearshore of the western sector of Algoa Bay (36 species representing 26 fish families) and by Tilney and Buxton (1994) further south in the Tsitsikamma National Park (55 species and 24 families).

Species of Gobiidae, Cynoglossidae, Engraulidae, Clupeidae, Sparidae, Blenniidae, Soleidae, Sciaenidae, Tripterygiidae and Kyphosidae larvae all made contributions of greater than 1 % towards the total larval fish catch in the present study. In the temperate waters of the Mediterranean, Sparidae, Blenniidae, Gobiidae and Tripterygiidae larvae similarly dominated shallow nearshore catches (Sabatés et al., 2003; Beldade et al., 2006). Similarly, in the tropical nearshore waters of Australia, New Zealand and Hawaii, larval gobiids, larbrids, sparids, clinids and tripterygiids dominate catches (Leis and Miller, 1976; Kingsford and Choat, 1989; Gray, 1993).

Larvae of Gobiidae dominated catches in the eastern and western (Beckley, 1986) sectors of Algoa Bay. The unidentified Gobiid 4 contributed ~29 % towards the overall larval fish catch. This family is the most diverse group of fish in southern Africa with over 100 species (Heemstra and Heemstra, 2004). High densities of goby larvae (15 larvae/m^3) mainly *Caffrogobius gilchristi* larvae are known to be flushed out of temperate estuaries in this region on the ebb tide (Beckley, 1985; Strydom and Wooldridge, 2005). This phenomenon could account for the high densities of goby species observed in this study, particularly in the shallower (~5 m) site just off the Sundays River mouth. Unfortunately, the larval stages of most gobiids in South Africa are not known and this species could not be identified. Together with Gobiid 4*,* *Engraulis capensis* and *Sardinops sagax* dominated catches in the shallow nearshore of the eastern sector of Algoa Bay. In the northwest Mediterranean, the European sardine and anchovy similarly dominate nearshore ichthyoplankton catches, however these two species have non-overlapping spawning periods in the northern hemisphere (Sabatés et al., 2007). A similar trend was observed in this study with densities of *S. sagax* greatest during summer and *E. capensis* densities greatest during spring.

Sardinops sagax, one of the key commercially important species of South Africa has undergone substantial population size fluctuations over the last 50 years (van der Lingen et al., 2006). Beckley (1986), recorded that the majority of *S. sagax* larvae caught within the shallow nearshore of the western sector of Algoa Bay were large with mean lengths of ~24 mm. Beckley (1986) suggested that *S. sagax* larvae were not spawned within the bay as this length corresponds to an age of nearly two months (Boyd and Badenhorst, 1981). The mean lengths from this study (~6 mm) however indicate a spawning area nearer the bay. Although densities of clupeids in this study are considerably lower than densities recorded by Beckley (1986), our results and the occurrence of larval *S. sagax* in estuary mouths in the bay (Strydom, 2003) do suggest that additional spawning occurs off the warm temperate coast.

Larvae of some threatened South African linefish species were found in this study including *Argyrosomus japonicus* and *A. thorpei*. The larvae of these commercially and recreationally important Sciaenidae species are rare in Eastern cape surf zones (Strydom and d'Hotman, 2005; Strydom, 2007) and isolated postflexion larvae and early juveniles of *A. japonicus* were recorded in the lower reaches of estuaries

(Beckley, 1983b; Beckley, 1984; Strydom et al., 2003; Strydom and Wooldridge, 2005). This suggests that the shallow nearshore is the preferential habitat for the larval stages of these species, and therefore plays a role as a primary nursery area, prior to recruitment to estuaries during the juvenile stage. Algoa Bay is known to be a major breeding area for *A. japonicus* (Smale, 1983). The preflexion stage was the dominant development stage observed in the sciaenid family in the present study. This supports the results from Smale (1983) as it is evident that spawning is occurring locally within the bay. Densities of sciaenid larvae peaked in spring and summer. Spring peaks in density of sciaenid larvae in the shallow nearshore (<30 m) has also been recorded in the southern gulf of Mexico (Espinosa-Fuentes and Flores-Coto, 2004).

In the study by Beckley (1986), sparid larvae only contributed 2 % to the total nearshore ichthyoplankton catch. In this study however, sparid larvae contributed 7 % to the total catch. Beckley (1986) suggested an “offshore” spawning and development of sparid larvae due to the low densities of early developmental stages recorded in the shallow (5 – 7 m) nearshore. In the present study, densities of early stage sparid larvae increased with distance from shore. As yet, it is not known where densities of sparid larvae peak relative to distance from shore. However, preflexion larvae of Sparidae were regularly encountered along the ~15 m depth contour in the present study which suggests that spawning is occurring closer to shore than that suggested by Beckley (1986).

Using Beckley’s (1986) classification of western Algoa Bay ichthyoplankton based on the distribution of adults and the type of eggs they produce, >50 % of the catch in the present study were coastal species that produce benthic eggs. Similarly larvae belonging to this group dominated catches (45 %) in the western sector of Algoa Bay in depths ranging from 5 – 7 m (Beckley, 1986). However, pelagic taxa producing pelagic eggs dominated catches (80 %) in the Tsitsikamma National Park, where larval fishes were collected in deeper water ranging from 20 – 80 m (Tilney and Buxton, 1994). A further trend observed in the present study was a decrease in the density of coastal species which produce benthic eggs with an increase in depth and distance from shore. In the shallow coastal nearshore waters of north-western Portugal (Azeiteiro et al., 2006) and central Chile (Hernández-Miranda et al., 2003), intertidal species including blenniids, clinids, gobiids and gobiesocids that produce benthic eggs occurred at their highest abundance in the zone nearest to the coast with abundance decreasing significantly away from shore. Nearshore larval assemblage studies from around the world show a similar trend with larvae from non-pelagic eggs most abundant close to shore (Leis and Miller, 1976; Leis, 1982; Marliave, 1986; Suthers and Frank, 1991; Sponaugle et al., 2003; Paris and Cowen, 2004).

A further trend observed in the present study was the dominance of marine species which are completely independent of estuaries. A similar trend was observed in subtropical KwaZulu-Natal where fish larvae found in the nearshore environment were mainly species which spawn in marine waters and are not dependent on estuaries (Harris et al., 1999; Harris et al., 2001). Conversely, in South African surf zones adjacent to the shallow nearshore, greater than 90 % of larval fish caught are estuary dependent (Harris and Cyrus, 1996; Strydom, 2003; Watt-Pringle and Strydom, 2003; Strydom and d'Hotman, 2005). Furthermore, in the shallow nearshore, marine species tend to occur in greater densities at the deeper (~15 m) depth contour.

5.2 Seasonal and spatial trends in larval fish

Densities of larval fishes were highest along the deeper ~15 m depth contour than just behind the surf zone (~5 m). Similar results were observed in subtropical KwaZulu-Natal (Harris et al., 1999) and in the Tsitsikamma National Park (Tilney and Buxton, 1994) where an increase in mean larval density occurred with an increase in the distance from shore. In the south-east Australian coastal waters, larval fish densities were greatest offshore (60 – 80 m deep) compared to inshore waters (30 m) (Gray and Miskiewicz, 2000) and in the north eastern coast of New Zealand (Tricklebank et al., 1992) densities of larval fishes were greatest offshore (3.2 km) than inshore (0.5 km).

Gradients in density of larval fishes with distance from shore are also accompanied by size gradients. A size gradient in larval fishes has been observed between the surf zone and the adjacent shallow nearshore (Harris et al., 1999; Strydom, 2007). Results from this present study support this work as higher percentages of larger larvae at the flexion and postflexion stage occurred at the shallower sites along the ~5 m depth contour. This is particularly evident in species that rely on sheltered coastal habitats such as estuaries for feeding and nurseries. These results support the shoreward movement hypothesis where larvae recruit from offshore spawning areas swimming towards appropriate coastal nursery habitats (Boehlert and Mundy, 1988). It seems that the shallow nearshore serves as a temporary accumulation area for larvae that will ultimately move into surf zones before swimming actively into estuary nursery areas (Boehlert and Mundy, 1988; Potter et al., 1990).

Highest densities, diversity and species richness of larval fishes were recorded in spring. This corresponds to the breeding season of coastal species with similar results observed in international studies (Raynie and Shaw, 1994; Palomera and Olivar, 1996; Sabatés et al., 2003; Azeiteiro et al., 2006; Borges et al., 2007). Temperature is known to be one of a suite of important environmental variables influencing larval fish assemblages in coastal waters (Kingsford, 1988; Tzeng and Wang, 1993; Harris et al., 1999). In temperate systems, larval fish density is usually higher in warmer, more saline months during spring and summer (Drake and Arias, 1991; Raynie and Shaw, 1994; Keller et al., 1999; Koutrakis et al., 2004; Azeiteiro et al., 2006). Lowest larval fish density was recorded in summer with similar results observed in the shallow nearshore waters of central Chile (Hernández-Miranda et al., 2003).

Seasonal changes in environmental variables were observed within the shallow nearshore but spatially the environment was fairly stable. Larval fish density in the present study displayed a high degree of both seasonal and spatial heterogeneity. Spatial variability in larval fish density can also be attributed to other environmental factors including upwelling and wind forcing (Pitts, 1999; Hernández-Miranda et al., 2003), current patterns (Cowen and Castro, 1994; Olivar and Beckley, 1994), type of water mass (Cowen et al., 1993; Chiu and Hsyu, 1994), the proximity of reefs (Kingsford and Choat, 1989; Tricklebank et al., 1992; Tilney and Buxton, 1994) and oceanographic conditions (Muhling and Beckley, 2007). The PCA demonstrated that water masses influence larval fish community structure, particularly since the majority of larvae were in a state of preflexion. The data showed a significant correlation between zooplankton and larval fish density with similar results recorded in other nearshore studies (Haldorson et al., 1992; Pedersen and Rice, 2002; Sabatés et al., 2007).

5.3 Developmental stage

The dominance of preflexion larvae within this study area suggests a high degree of local production occurring in the area. Marine species (category III) were generally found to occur in higher densities along the deeper ~15 m depth contour than the shallow sites behind the surf zone and were dominated by preflexion larvae. *Engraulis capensis* and *Sardinops sagax* are pelagic fish that usually occur over the continental shelf to depths of ~200 m. Spawning of these species occurs on the south and east coast of South Africa, particularly on the Agulhas Bank, south of Algoa Bay (Heemstra and Heemstra, 2004). Juveniles of the sciaenid, *Argyrosomus thorpei*, are known to occur on soft bottoms in 15-50 m with adults occurring on rocky reefs and sand to depths of 80 m (Heemstra and Heemstra, 2004). The tripterygiid *Cremnochorites capensis* is known to occur in rocky reefs in depths of 20-30 m (Heemstra and Heemstra, 2004). *Cynoglossus zanzibarensis* occurs on sandy or silty sand bottom in depths from 10-430 m and spawns pelagic eggs (Heemstra and Heemstra, 2004). The sparid, *Spondyliosoma emarginatum*, produces benthic eggs that are deposited in depressions on the sandy bottom in depths of 2–60 m (Heemstra and Heemstra, 2004). Juvenile kyphosids are known to occur in the open ocean with *Sargassum* weed or floatsam (Heemstra and Heemstra, 2004). The presence of all developmental stages (preflexion, flexion and postflexion) of certain blenniids, clupeids, engraulids, gobiesocids, gobiids, haemulids, soleids, sparids and tripterygiids within the study area suggests that the pelagic phase of these larval fishes is completed within the shallow nearshore. It has been suggested that remaining inshore is advantageous to finding a suitable settlement habitat at the end of the larval stage (Hickford and Schiel, 2003). The proposed MPA is therefore situated in a functioning spawning and nursery area for many coastal fish species.

6. CONCLUSION

This study has highlighted the high ichthyoplankton diversity and species richness that occurs in the shallow nearshore of the eastern sector of Algoa Bay. Preflexion larvae dominated catches in this study suggesting a high degree of local hatching occurring in the area, specifically for important recreational linefish and commercial species particularly species such as *A. japonicus*, *A. thorpei*, *D. capensis*, *E. capensis* and *S. sagax*. The presence of the early developmental stages of commercially and recreationally important species that occur in surf zones and estuaries as postflexion larvae and early juveniles, suggests that the shallow nearshore provides adjacent coastal nursery areas with larval recruits. The shallow nearshore of eastern Algoa Bay can therefore be regarded as an important nursery area. This study has provided baseline information on species composition, seasonality, distribution and abundance in an area to be declared a marine reserve. This project creates an ideal comparative base for the area which will allow for comparisons and monitoring once the reserve is proclaimed and fish stocks recover.

7. ACKNOWLEDGEMENTS

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8. REFERENCES CITED

AZEITEIRO, U.M., BACHELAR-NICOLAU, L., RESENDE, P., GONÇALVES, F., PEREIRA, M.J. 2006. Larval fish distribution in shallow coastal waters off North Western Iberia (NE Atlantic). *Estuarine, Coastal and Shelf Science* **69**: 554-566.

BECKLEY, L.E. 1983a. Sea-surface temperature variability around Cape Recife, South Africa. *South African Journal of Science* **79**: 436-438.

BECKLEY, L.E. 1983b. The ichthyofauna associated with *Zostera capensis* Setchell in the Swartkops estuary, South Africa. *South African Journal of Zoology* **18**: 15-24.

BECKLEY, L.E. 1984. The ichthyofauna of the Sundays estuary, South Africa, with particular reference to the juvenile marine component. *Estuaries* **7**: 248-258.

BECKLEY, L.E. 1985. Tidal exchange of ichthyoplankton in the Swartkops Estuary mouth, South Africa. *South African Journal of Zoology* **20**: 15-20.

BECKLEY, L.E. 1986. The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. *South African Journal of Zoology* **21**: 244-252.

BECKLEY, L.E. 1988. Spatial and temporal variability in sea temperatures in Algoa Bay, South Africa. *South African Journal of Science* **84**: 67-69.

BELDADE, R., BORGES, R., GONÇALVES, E.J. 2006. Depth distribution of nearshore temperate fish larval assemblages near rocky substrates. *Journal of Plankton Research* **28**: 1003-1013.

BOEHLERT, G.W., MUNDY, B.C. 1988. Roles of behaviour and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* **3**: 51-67.

BORGES, R., BEN-HAMADOU, R., ALEXANDRA CHÍCHARO, M., RÉ, P., GONÇALVES, E.J. 2007. Horizontal spatial and temporal distribution patterns of nearshore larval fish assemblages at a temperate rocky shore. *Estuarine, Coastal and Shelf Science* **71**: 412-428.

BOYD, A.J., BADENHORST, A. 1981. A note on the early growth of pilchard *Sardinops ocellata* larvae. *Fishery Bulletin of South Africa* **15**: 43-48.

CHIU, T.S., HSYU, Y.I. 1994. Interannual variation of ichthyoplankton density and species composition in the waters off northeastern Taiwan. *Marine Biology* **119**: 441-448.

CHUTE, A.S., TURNER, J.T. 2001. Plankton studies in Buzzards Bay, Massachusetts, USA.V. Ichthyoplankton, 1987 to 1993. *Marine Ecology Progress Series* **224**: 45-54.

CLARKE, K.R., WARWICK, R.M. 1994. Change in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth 144 pp.

COWEN, R.K., CASTRO, L.R. 1994. Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. *Bulletin of Marine Science* **54**: 228-244.

COWEN, R.K., HARE, J.A., FAHAY, M.P. 1993. Beyond hydrography: can physical processes explain larval fish assemblages within the middle Atlantic Bight? *Bulletin of Marine Science* **53**: 567-587.

DOHERTY, P., MCILWAIN, J. 1996. Monitoring larval fluxes through the surf zones of Australian coral reefs. *Marine and Freshwater Research* **47**: 383-390.

DRAKE, P., ARIAS, A.M. 1991. Composition and seasonal fluctuations of the ichthyoplankton community in a shallow tidal channel of Cadiz Bay (S.W. Spain). *Journal of Fish Biology* **39**: 245-263.

ELLIOTT, M., O'REILLY, M.G., TAYLOR, C.J.L. 1990. The Forth estuary: a nursery and overwintering area for North Sea fishes. *Hydrobiologia* **195**: 989-103.

ESPINOSA-FUENTES, M.L., FLORES-COTO, C. 2004. Cross-shelf vertical structure of ichthyoplankton assemblages in continental shelf waters of the Southern Gulf of Mexico. *Estuarine, Coastal and Shelf Science* **59**: 333-352.

GOSCHEN, W.S., SCHUMANN, E.H. 1995. Upwelling and the occurrence of cold water around Cape Recife, South Africa. *South African Journal of Marine Science* **16**: 57-67.

GRAY, C.A. 1993. Horizontal and vertical trends in the distribution of larval fishes in coastal waters off central New South Wales, Australia. *Marine Biology* **116**: 649-666.

GRAY, C.A. 1996. Small-scale temporal variability in assemblages of larval fishes: implications for sampling. *Journal of Plankton Research* **18**: 1643-1657.

GRAY, C.A., MISKIEWICZ, A.G. 2000. Larval fish assemblages in south-east Australian coastal waters: seasonal and spatial structure. *Estuarine, Coastal and Shelf Science* **50**: 549-570.

HALDORSON, L., PRICHETT, D., STERRITT, D., WATTS, J. 1992. Abundance patterns of marine fish larvae during spring in a southeastern Alaskan bay. *Fishery Bulletin* **91**: 36-44.

HARRIS, S.A., CYRUS, D.P. 1996. Occurrence of larval fish in the surf zone adjacent to the St Lucia Estuary mouth, KwaZulu-Natal, South Africa. *Marine and Freshwater Research* **47**: 465-482.

HARRIS, S.A., CYRUS, D.P., BECKLEY, L.E. 1999. The larval fish assemblage in the nearshore coastal waters off the St Lucia Estuary, South Africa. *Estuarine, Coastal and Shelf Science* **49**: 789-811.

HARRIS, S.A., CYRUS, D.P., BECKLEY, L.E. 2001. Horizontal trends in larval fish diversity and abundance along an ocean-estuarine gradient on the Northern KwaZulu-Natal Coast, South Africa. *Estuarine, Coastal and Shelf Science* **53**: 221-235.

HARRIS, T.F.W. 1978. Review of coastal currents in South African wasters. *South African National Scientific Programmes Report* **30**: 1-103.

HEEMSTRA, P.C., HEEMSTRA, E. 2004. Coastal fishes of Southern Africa. South African Institute for Aquatic Biodiversity and National Inquiry Service Centre, Grahamstown 488 pp.

HERNÁNDEZ-MIRANDA, E., PALMA, A.T., OJEDA, F.P. 2003. Larval fish assemblages in nearshore coastal waters off central Chile: temporal and spatial patterns. *Estuarine, Coastal and Shelf Science* **56**: 1075-1092.

HICKFORD, M.J.H., SCHIEL, D.R. 2003. Comparative dispersal of larvae from demersal versus pelagic spawning fishes. *Marine Ecology Progress Series* **252**: 255-271.

JENNINGS, S. 2000. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries* **10**: 209-231.

KELLER, A.A., KLEIN-MACPHE, G., BURNS, J.S.O. 1999. Abundance and distribution of ichthyoplankton in Narragansett Bay, Rhode Island, 1989-1990. *Estuaries* **22**: 149-163.

KINGSFORD, M.J. 1988. The early life history of fish in coastal waters of northern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* **22**: 463-479.

KINGSFORD, M.J., CHOAT, J.H. 1989. Horizontal distribution patterns of presettlement reef fish: are they influenced by the proximity of reefs? *Marine Biology* **101**: 285-297.

KOUTRAKIS, E.T., KALLIANIOTIS, A.A., TSIKIRAS, A.C. 2004. Temporal patterns of larval fish distribution and abundance in a coastal area of northern Greece. *Sciencia Marina* **68**: 585-595.

LEIS, J.M. 1982. Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawaii. *Marine Biology* **72**: 89-97.

LEIS, J.M. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes. Academic Press, New York 183-230.

LEIS, J.M. 2003. What does the larval fish biology tell us about the design and efficacy of marine protected areas. Aquatic protected areas: What works best and how do we know? Australian Society for Fish Biology, North Beach, WA pp. 170-180,

LEIS, J.M., CARSON-EWART, B.M. 2000. The larvae of Indo-Pacific coastal fishes: An identification guide to marine fish larvae. Koninklijke Brill, Leiden 850 pp.

LEIS, J.M., MILLER, J.M. 1976. Offshore distributional patterns of Hawaiian fish larvae. *Marine Biology* **36**: 359-367.

LOTZE, H.K. 2007. Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. *Fisheries Research* **87**: 208-218.

LUTJEHARMS, J.R.E. 1981. Features of the southern Agulhas Current circulation from satellite remote sensing. *South African Journal of Science* **77**: 231-236.

MARLIAVE, J.B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. *Transactions of American Fisheries Society* **115**: 149-154.

MERCADO, J.M., CORTÉS, D., GARCÍA, A., RAMÍREZ, T. 2007. Seasonal and inter-annual changes in the planktonic communities of the northwest Alboran Sea (Mediterranean Sea). *Progress in Oceanography* **74**: 273-293.

MOSER, H.G., RICHARDS, W.J., COHEN, D.M., FAHAY, M.P., KENDALL, A.W., RICHARDSON, S.L. 1984. Ontogeny and systematics of fishes. *American Society of Ichthyologists and Herpetologists Special Publication* **1**: 1-760.

MUHLING, B.A., BECKLEY, L.E. 2007. Seasonal variation in horizontal and vertical structure of larval fish assemblages off south-western Australia, with implications for larval transport. *Journal of Plankton Research* **29**: 967-983.

MYERS, R.A., WORM, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**: 280-283.

NEIRA, F.J., MISKIEWICZ, A.G., TRNSKI, T. 1998. Larvae of Temperate Australian fishes. Laboratory guide for larval fish identification. University of Western Australia Press, Nedlands 474 pp.

OKIYAMA, M. 1988. An atlas of the early stage fishes in Japan. Tokai University Press, Tokyo 1154 pp.

OLIVAR, M.P., BECKLEY, L.E. 1994. Influence of the Agulhas Current on the distribution of lanternfish larvae off the southeast coast of Africa. *Journal of Plankton Research* **16**: 1759-1780.

OLIVAR, M.P., FORTUÑO, J.M. 1991. Guide to ichthyoplankton of the southeast Atlantic (Benguela Current Region). *Sciencia Marina* **55**: 1-383.

PALOMERA, I., OLIVAR, M.P. 1996. Nearshore ichthyoplankton off the Costa Brava (northwest Mediterranean Sea). *Publicaciones Especiales de Instituto Español de Oceanografía* **22**: 71-75.

PARIS, C., COWEN, R.K. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography* **49**: 1964-1979.

PEDERSEN, S.A., RICE, J.C. 2002. 5 Dynamics of fish larvae, zooplankton, and hydrographical characteristics in the West Greenland large marine ecosystem 1950 - 1984. *Large Marine Ecosystems* **10**: 151-193.

PITTS, P.A. 1999. Effects of summer upwelling on the abundance and vertical distribution of fish and crustacean larvae of central Florida's Atlantic coast. *Journal of Experimental Biology and Ecology* **235**: 135-146.

POTTER, I.C., BECKLEY, L.E., WHITFIELD, A.K., LENANTON, R.C.J. 1990. Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa. *Environmental Biology of Fishes* **28**: 143-178.

RAYNIE, R.C., SHAW, R.F. 1994. Ichthyoplankton abundance a recruitment corridor from offshore spawning to estuarine nursery ground. *Estuarine, Coastal and Shelf Science* **39**: 421-450.

RICHARDS, W.J. 2005. Early stages of Atlantic fishes: an identification guide for the western central north Atlantic. Taylor & Francis, Florida 2640 pp.

SABATÉS, A., OLIVAR, M.P., SALAT, J., PALOMERA, I., ALEMANY, F. 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography* **74**: 355-376.

SABATÉS, A., ZABALA, M., GARCÍA-RUBIES, A. 2003. Larval fish communities in the Medes Islands Marine Reserve (North-west Mediterranean). *Journal of Plankton Research* **24**: 1035-1046.

SCHAFER, L.N., PLATELL, M.E., VALESINI, F.J., POTTER, I.C. 2002. Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. *Journal of Experimental Marine Biology and Ecology* **278**: 67-92.

SCHUMANN, E.H. 1987. The coastal ocean off the east coast of South Africa. *Transactions of the Royal Society of South Africa* **46**: 215-228.

SCHUMANN, E.H. 1998. The coastal ocean off southeast Africa, including Madagascar. *The Sea* **11**: 557-582.

SCHUMANN, E.H., CHURCHILL, J.R.S., ZAAYMAN, H. 2005. Oceanic variability in the western sector of Algoa Bay, South Africa. *African Journal of Marine Science* **27**: 65-80.

SCHUMANN, E.H., MARTIN, J.A. 1991. Climatological aspects of the coastal windfield at Cape Town, Port Elizabeth and Durban. *South African Geographical Journal* **73**: 48-51.

SCHUMANN, E.H., ROSS, G.J.B., GOSCHEN, W.S. 1988. Cold water events in Algoa Bay and along the Cape south coast, South Africa, in March/April 1987. *South African Journal of Science* **84**: 579-583.

SENTA, T., KINOSHITA, I. 1985. Larval and juvenile fishes occurring in surf zones of western Japan. *Transactions of the American Fisheries Society* **114**: 609-618.

SMALE, M.J. 1983. Resource partitioning by top predatory teleosts in eastern Cape coastal waters (South Africa). Ph.D. thesis, Rhodes University, South Africa,

SMITH, M.M., HEEMSTRA, P.C. 1995. Smith's Sea Fishes. Macmillan, Johannesburg, South Africa. 1047pp.

SPONAUGLE, S., FORTUNA, J., GRORUD, K., LEE, T. 2003. Dynamics of larval fish assemblages over a shallow coral reef in the Florida Keys. *Marine Biology* **143**: 175-189.

STRYDOM, N.A. 2003. Occurrence of larval and early juvenile fishes in the surf zone adjacent to two intermittently open estuaries, South Africa. *Environ Biol Fish* **66**: 349-359.

STRYDOM, N.A. 2007. Jetski-based plankton towing as a new method of sampling larval fishes in shallow marine habitats. *Environmental Biology of Fishes* **78**: 299-306.

STRYDOM, N.A., D'HOTMAN, B.D. 2005. Estuary-dependence of larval fishes in a non-estuary associated South African surf zone: evidence for continuity of surf assemblages. *Estuarine, Coastal and Shelf Science* **63**: 101-108.

STRYDOM, N.A., WHITFIELD, A.K., WOOLDRIDGE, T.H. 2003. The role of estuarine type in characterizing early stage fish assemblages in warm temperature estuaries, South Africa. *African Zoology* **38**: 29-43.

STRYDOM, N.A., WOOLDRIDGE, T.H. 2005. Diel and tidal variations in larval fish exchange in the mouth region of the Gamtoos Estuary, South Africa. *African Journal of Aquatic Science* **30**: 131-140.

SUTHERS, I.M., FRANK, K.T. 1991. Comparative persistence of marine fish larvae from pelagic versus demersal eggs off southwestern Nova Scotia, Canada. *Marine Biology* **108**: 175-184.

SVEDÄNG, H., BARDON, G. 2003. Spatial and temporal aspects of the decline in cod (*Gadus morhua* L.) abundance in the Kattegat and eastern Skagerrak. *ICES Journal of Marine Science* **60**: 32-37.

TILNEY, R.L., BUXTON, C.D. 1994. A preliminary ichthyoplankton survey of the Tsitsikamma National Park. *South African Journal of Zoology* **29**: 204-211.

TRICKLEBANK, K.A., JACOBY, C.A., MONTGOMERY, J.C. 1992. Composition, distribution and abundance of neustonic ichthyoplankton off northeastern New Zealand. *Estuarine, Coastal and Shelf Science* **34**: 263-275.

TZENG, W.N., WANG, Y.T. 1993. Hydrography and distribution dynamics of larval and juvenile fishes in the coastal waters of the Tanshui River estuary, Taiwan, with reference to estuarine larval transport. *Marine Biology* **116**: 205-217.

VAN DER LINGEN, C.D., FRÉON, P., FAIRWEATHER, T.P., VAN DER WESTHUIZEN, J.J. 2006. Density-dependent changes in reproductive parameters and condition of southern Benguela sardine *Sardinops sagax*. *African Journal of Marine Science* **28**: 625-636.

WATT-PRINGLE, P., STRYDOM, N.A. 2003. Habitat use by larval fishes in a temperate South African surf zone. *Est Coast Shelf Sci* **58**: 765-774.

WHITFIELD, A.K. 1989. Ichthyoplankton in a southern African surf zone: Nursery area for the postlarvae of estuarine associated fish species? *Estuarine, Coastal and Shelf Science* **29**: 533-547.

WHITFIELD, A.K. 1998. Biology and ecology of fishes in South African Estuaries. Ichthyological Monographs of the JLB Smith Institute for Ichthyology, No. **2**: Grahamstown 232 pp.

YOUNG, P.C., LEIS, J.M., HAUSFELD, H.F. 1986. Seasonal and spatial distribution of fish larvae in waters over the north west continental shelf of Western Australia. *Marine Ecology Progress Series* **31**: 209-222.

CHAPTER 3

NEARSHORE CURRENTS AND THEIR POTENTIAL EFFECTS ON DISPERSAL OF FISH EGGS AND LARVAE IN THE PROPOSED GREATER ADDO MARINE RESERVE, ALGOA BAY, SOUTH AFRICA

1. SYNOPSIS

An Acoustic Doppler Current Profiler (ADCP) was used to measure current direction and velocity in the shallow nearshore of a proposed marine protected area in Algoa Bay, South Africa. The purpose of the study was to describe the shallow water dynamics with emphasis on the potential influence on eggs and larval fishes occurring in the area. One-day profiling surveys as well as data from a bottom-moored ADCP were used to describe current flow patterns. Three different flow patterns were identified from seven one-day profiling surveys conducted in the nearshore behind a dissipative beach surf zone, between depths of 4 – 20 m. The first pattern was characterized by eastward flow, the second pattern was characterized by westward flow and the third pattern consisted of mixed east-west flows. Analysis of 12 months (May 2006 – May 2007) of half-hourly collected data from a bottom-moored ADCP on the 15 m depth contour showed that within the nearshore, the offshore flowing south eastward (39 %) and onshore flowing north westward (33 %) currents occurred more frequently than the south westward (15 %) and north eastward (13 %) currents. Modal current velocity near the surface of the water column (4 m) was 8 cms^{-1} and near the bottom of the water column (14 m) was 6 cms^{-1}. Velocity decreased with depth in the nearshore, with a mean velocity of ~30 cms^{-1} recorded at a depth of 4 m and a mean velocity of ~10 cms^{-1} recorded at a depth of 14 m. Potential net displacements indicate that eggs and preflexion larvae would likely be transported eastwards, reaching distances of 84 km near the surface (4 m) and 24 km at the bottom (14 m) of the water column in winter over a period of three months. Over a similar period of time during the peak breeding season of fishes during spring and early summer, distances of 110 km near the surface and 186 km at the bottom of the water column can occur. The complexities of the larval phase, particularly postflexion stage swimming abilities, are discussed within the context of Algoa Bay.

2. INTRODUCTION

Algoa Bay, situated on the south-east coast of South Africa, is a wide, shallow bay with depths not exceeding 70 meters (Schumann et al., 2005). Most oceanographic studies in the Bay to date have been confined to the western sector (CSIR, 1970; Roberts, 1990) or in waters exceeding depths of 20 m (Harris, 1978; Lutjeharms et al., 1986; Goschen and Schumann, 1988; Boyd et al., 1992; Goschen and Schumann, 1994; Boyd and Oberholster, 1994). Oceanographic research in the eastern part of Algoa Bay is limited, particularly in shallow waters (<20 m) where most coastal fish nurseries occur (Chute and Turner, 2001). This is the first study in the eastern sector of Algoa Bay where an Acoustic Doppler Current Profiler (ADCP) was used to measure shallow (4 – 20 m) nearshore currents.

Within the western sector of Algoa Bay, a survey completed by the Hydraulics Research Unit of the National Mechanical Engineering Research Institute of the CSIR between November 1967 and November 1968, reported that the deep water (30 m) nearshore currents were very week (< 8 cms^{-1}) with north-easterly winds creating very weak (0 – 8 cms^{-1}) flowing currents. Without the interference of wind, currents were very weak and in a southerly direction (CSIR, 1970). Roberts (1990) examined the nearshore surface currents within the western bight of Algoa Bay via the dispersion of pollutants from the shoreline. Surface currents were found to respond primarily to the influence of the local wind. In offshore studies, Harris (1978) followed by Lutjeharms et al. (1986) observed north-eastward and south-westward surface currents equally dominating in the centre of Algoa Bay (~50 m depth). Current velocities were reported to range between 20 – 40 cms^{-1} and were influenced by wind direction. Goschen and Schumann (1988) using a hydrosonde, observed little variation in current speed and direction with depth (surface – 100 m) offshore of Algoa Bay during early summer. Currents flowed predominantly north-eastwards in the direction of the prevailing south-westerly winds.

Currents play an important role in determining the distribution of larval fishes (Leis and Goldman, 1983) along with the larval stages of most invertebrate fauna, other zooplankton and phytoplankton (Mackas et al., 1985). The behaviour of larval fishes together with the dynamics of the water body in which they occur, need to be understood in order to assess the influence of ocean currents on larvae and to determine the net dispersal of larvae (Leis, 2006). With the swimming abilities of larval fish now known (Stobutzki and Bellwood, 1994; Leis et al., 1996; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997), data suggests that mid to late stage larvae are not passive particles in the water column but active swimmers, with keen sensory abilities (Kingsford et al., 2002) able to select preferred habitats and maintain their position there (Melville-Smith et al., 1981; Boehlert and Mundy, 1988; Leis et al., 1996; Leis and Carson-Ewart, 1998; Leis and Carson-Ewart, 1999; Leis and Carson-Ewart, 2001; Watt-Pringle and Strydom, 2003), thereby aiding and directing dispersal. The interaction between larval fish biology and oceanography is complex yet essential in the understanding of dispersal of larvae and how this effects fish populations (Kinlan and Gaines, 2003; Palumbi, 2003; Sale, 2004). More recently larval fish dynamics are being used to assess and question the efficacy and design of marine conservation areas such as marine protected areas (MPAs) (Leis, 2003; Leis, 2006).

A new MPA is planned for the eastern sector of Algoa Bay. The objective of the present study was to describe current direction and velocity patterns within the shallow nearshore zone of the proposed MPA using data collected from one-day profiling surveys and a long-term (12 months) moored ADCP survey. Nearshore areas are known accumulation and nursery areas for coastal fishes (Leis, 1982; Beckley, 1986; Palomera and Olivar, 1996; Sponaugle and Cowen, 1996; Harris et al., 1999; Hernández-Miranda et al., 2003; Borges et al., 2007). Data generated from these surveys were used to discuss the potential transport of fish eggs and preflexion larval fishes to and from the reserve area.

3. MATERIALS AND METHODS

3.1 Study site

Algoa Bay is situated on the south east coast of South Africa (Fig. 3.1) and is a wide (~80 km), eastward-facing bay with depths not exceeding 70 meters (Harris, 1978; Roberts, 1990). Algoa Bay is situated in the warm-temperate region of South Africa and receives peak rainfall in autumn and spring (Whitfield, 1998). The Agulhas Current flows along the edge of the continental shelf in a south-westwards direction approximately 80 kms offshore of Algoa Bay (Lutjeharms, 1981) with subtropical waters from the current occasionally entering the bay (Schumann, 1987). South-westerly winds dominate across the bay throughout the year (Schumann and Martin, 1991). In summer the frequency of easterly winds increases creating upwelling at Cape Recife to the west, with this colder water (by about 8 °C) moving westwards (Schumann et al., 1988). Westerly winds can however bring this colder upwelled water into the bay (Goschen and Schumann, 1995). Temperatures in the bay range from ~11 °C in winter to ~27 °C in summer (Beckley, 1983; Beckley, 1988). Intense thermoclines are established in summer in the deeper sections of the bay with isothermal conditions occurring in winter. With minimal freshwater inflow into the bays from rivers, the salinity within the bay is stable, with an average of about 35.2 (Schumann, 1998; Schumann et al., 2005).

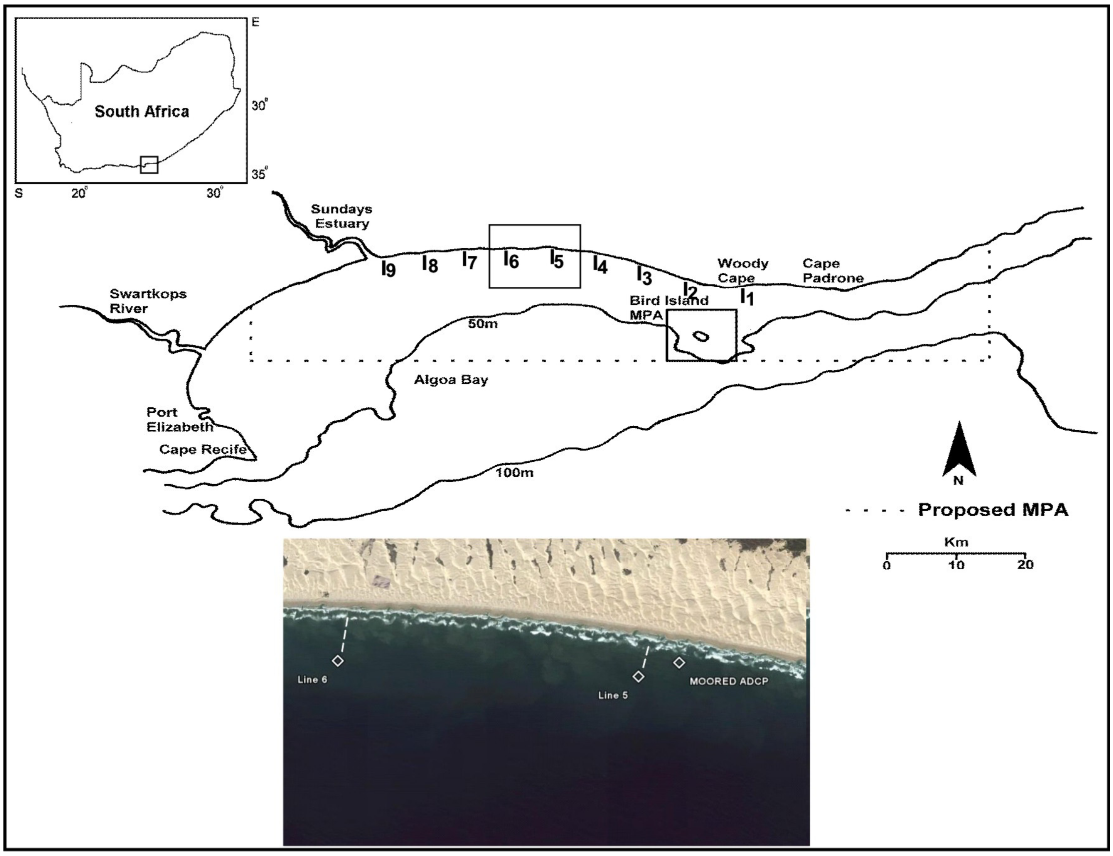


Figure 3.1: The geographical position of Algoa Bay, showing the position of the nine ADCP transect lines and a satellite image showing the position of the bottom-moored (15 m) ADCP (Google Earth)

3.2 Field sampling

One-day profiling surveys

Collection of current data was conducted by oceanographic technicians from Marine and Coastal Management, South Africa. Sampling took place during eight one-day profiling surveys, four in winter and four in summer between August 2005 and February 2007. One survey was cancelled due to arduous sea conditions resulting in only three surveys in summer. A 300 kHz ADCP (*RD Instruments* of San Diego, California), mounted onto a small boat (7.3 m) was used to survey nine transect lines, which ran perpendicular to the shore from the 20 m depth contour to just behind the surf backline (4 m), between Woody Cape (33°46’709’’S, 26°20’281’’E) and Sundays Estuary (33°44’205’’S, 25°51’562”E) (Fig. 3.1). Transect lines were placed at intervals of 4 kms. Line 1 was the longest transect line with a length of ~3000 m, while line 6 was the shortest transect line with a length of ~400m. These surveys were conducted over the course of three fieldtrips.

Moored ADCP

An ADCP was also moored in the centre of the study area (Fig. 3.1), on the 15 m depth contour for a period of one year between May 2006 and May 2007. The ADCP was configured to record every 30 minutes using an ensemble size of 120 pings, with one ping used per second. The water column was sampled using 15 bins each of 1 m depth, between the surface and 14 m. Prior to processing, data in each bin was checked for quality (Fig. 3.2). For this analysis, only bins in which >75 % of the readings were ‘good’ were used (Gordon, 1996). This eliminated the surface, 1 m, 2 m and 3 m bins.

Wind data were obtained at hourly intervals from three *South African Weather Bureau* stations located on Bird Island (3 m above sea level), on the eastern boundary of the study area, at Port Elizabeth Harbour (63 m above sea level) and at Coega Harbour (46 m above sea level) on the western boundary of the study area. Wind data was collected for a period of one year between May 2006 and May 2007.

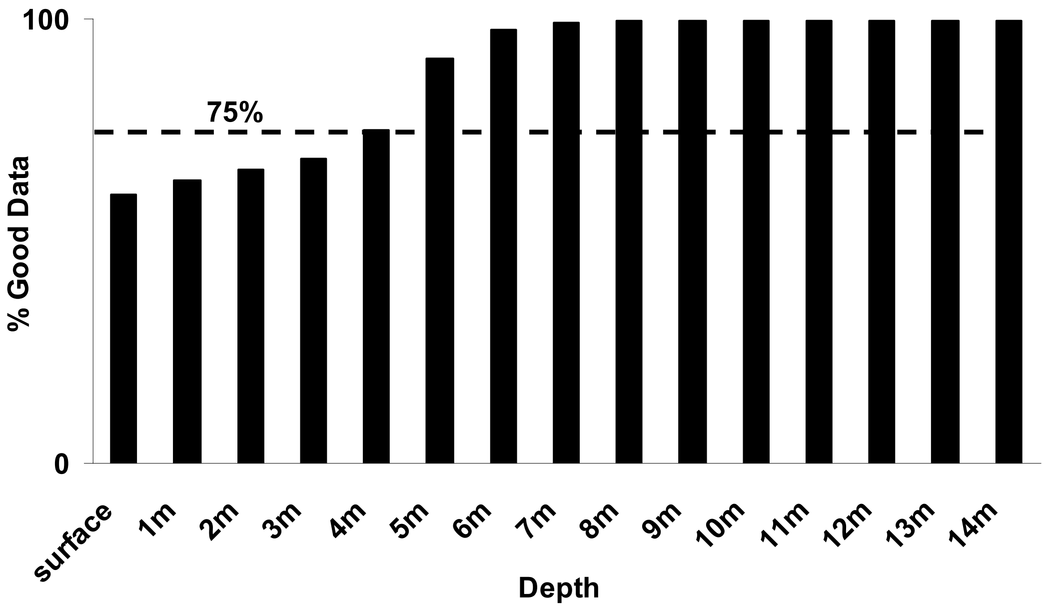


Figure 3.2: The quality of the data from the bottom-moored ADCP on the 15 m depth contour in the shallow nearshore of eastern Algoa Bay showing the percentage of good data at each depth

3.3 Data analyses

Current velocity, current direction, wind speed and wind direction data were tested for normality and homogeneity of variance using a normal probability plot, Shapiro-Wilk test and Levene's test and conformed to parametric test assumptions. Current velocity and direction data was correlated with wind speed and direction data respectively using simple linear (Pearson r) correlation. Potential transport of eggs and preflexion larvae was calculated by combining the east-west and north-south velocity components providing total progressive displacement.

4. RESULTS

4.1 One-day profiling surveys

Three different flow patterns were observed within the shallow nearshore during the one-day profiling surveys (Figs 3.3 and 3.4). The first pattern, a strong westward current characterized by uni-directional flow throughout the water column was observed on the 03/08/2005, 04/08/2005 and 20/02/2007, with current velocities ranging from 0 to ~30 cms^{-1}. The second pattern, an eastward flow ranging in velocity from 0 to 12 cm^{-1}, was observed on the 25/05/2006 and similarly an eastward flow occurred on the 18/02/2007 ranging in velocity from 0 to ~30 cm^{-1}. A third pattern, characterized by mixed east-west flows occurred on the 24/05/2006 with velocities ranging from 0 to ~25 cm^{-1}. On the 24/05/2006 currents flowed in a westward direction at Lines 1 – 3 and 9 and in an eastward direction at Lines 4 – 8 at both the surface (Fig. 3.3) and at the bottom of the water column (Fig. 3.4). No clear flow pattern was observed on the 19/02/2007.

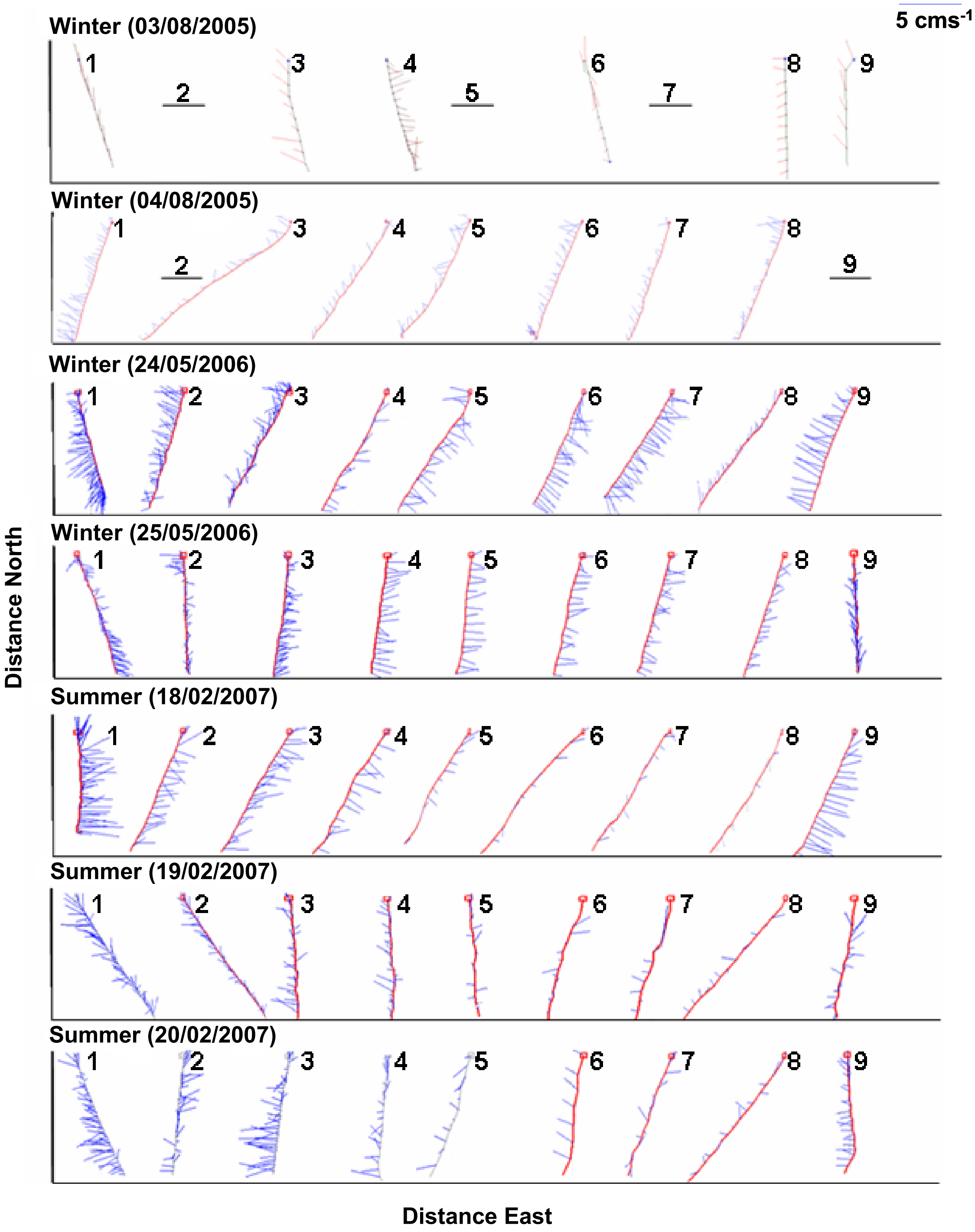


Figure 3.3: Vector plots of near surface current flow (4 m) showing direction and velocity at each transect line on each day of the ADCP one-day profiling surveys. Note: Instrumental error in data for lines 2, 5 and 7 on the 03/08/2005 and at lines 2 and 9 on the 04/08/2005. Figure supplied by Marine and Coastal Management, Cape Town South Africa

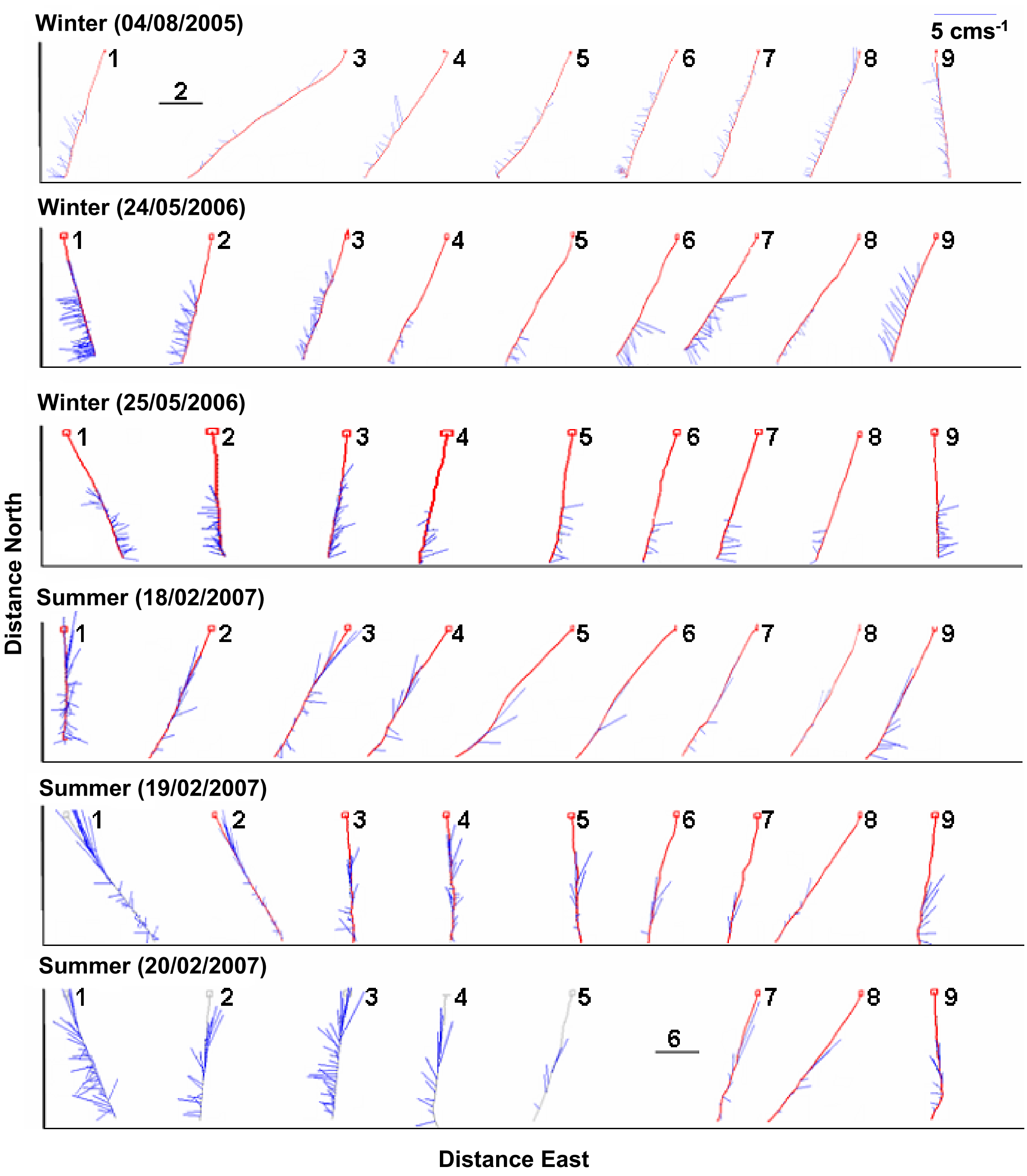


Figure 3.4: Vector plots of near bottom current flow (14 m) showing direction and velocity at each transect line on each day of the ADCP one-day profiling surveys. Note: Instrument error in data for line 2 on the 04/08/2005 and line 6 on the 20/02/2007. Please note no transect data collected for the bottom of the water column on 03/08/2005. Figure supplied by Marine and Coastal Management, Cape Town South Africa

Some of the complexity of the nearshore flow regime is highlighted in Figure 3.5. For example, at Line 2 on the 25/05/06 (Fig. 3.5.a) higher current velocities (~10 cms^{-1}) were observed in the shallow water just behind the backline than water at a depth of 20 m (~5 cms^{-1}). Current velocities within the water column were generally observed to flow either uniformly or with a slight decreasing trend from the surface to the bottom of the water column. However, there were periods when current velocities were highest in the bottom layer of the water column e.g. Fig 3.5.b (Line 2; 24/05/06). Furthermore in Figure 3.5.b the higher current velocities do extend into the surface layer of the water column close to shore, just behind the backline, at a depth of <13 m. A reversal in this pattern was observed at Line 5 on the 25/05/06 (Fig. 3.5.c), when current velocities were greatest in the surface layer. Figure 3.5.d shows a situation where different current directions were observed between the surface and bottom water. The surface layer flows in a westward direction and the bottom layer flows eastwards (Line 8; 24/05/06).

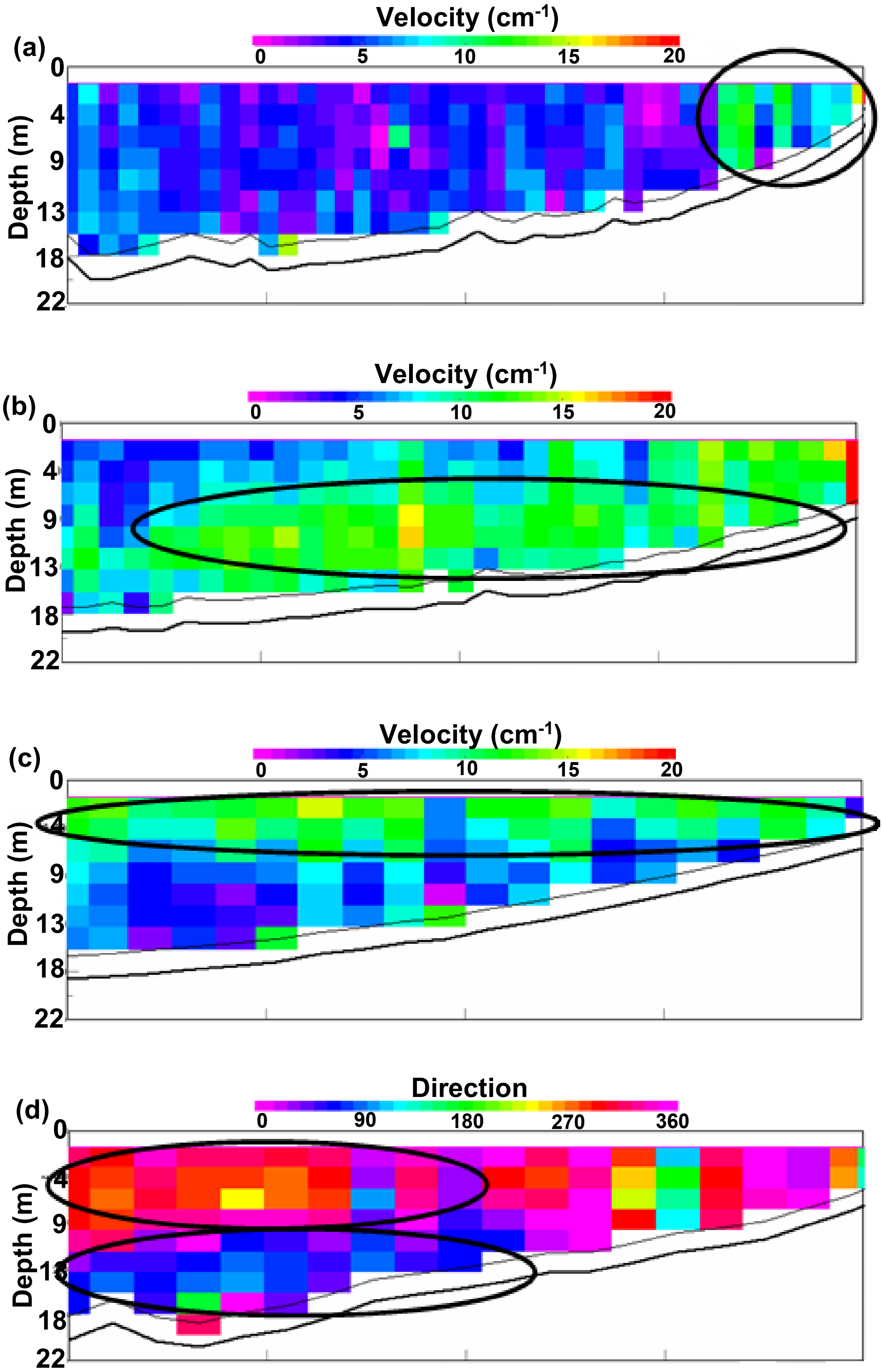


Figure 3.5: Characteristics of the shallow nearshore current environment highlighted during the one-day profiling surveys: (a), Higher velocities (~10 cm^{-1}) recorded in the shallower nearshore than the adjacent deeper nearshore (~5 cm^{-1}) (Line 2; 25/05/06) (b), The bottom of the water column has a higher velocity of ~10 cm^{-1} while the surface has a slower velocity of ~5 cm^{-1} (Line 2; 24/05/06) (c), The surface layer has a higher velocity of ~10 cm^{-1} while the bottom layer has a slower velocity of ~5 cm^{-1} (Line 5; 25/05/06) (d), Bottom layer in the deeper nearshore flows west while the surface layer flows northwest (Line 8; 24/05/06). Figure supplied by Marine and Coastal Management, Cape Town South Africa

4.2 Moored ADCP survey

Figure 3.6 shows the entire 12 months (May 2006 – May 2007) of (a) current direction and (b) velocity data collected by the bottom-moored ADCP. The direction data showed two dominant flow patterns, an offshore south eastward flow and an onshore north westward flow. Near the surface of the water column, the south eastward flow was found to persist for 36 % of the time while the north westward flow occurred 32 % of the time (Fig. 3.7.a). The south westward flow (18 %) and the north eastward flow (14 %) occurred less frequently during the study period near the surface of the water column. Similar flow direction was observed at the bottom of the water column with the south eastward flow occurring 40 % of the time and the north westward flow occurring 32 % of the time (Fig. 3.7.b). As with the surface pattern, the south westward flow (15 %) and the north eastward flow (13 %) occurred less frequently during the study period at the bottom of the water column. The south eastward flow dominated flow throughout the year except during the winter months of June 2006 and July 2006 and during May 2007, when the north westward current dominated only slightly over the south eastward current. In terms of wind direction, the south westerly winds dominated (48 %) during the study period (May 2006 – May 2007) (Fig. 3.7.c). The south easterly (21 %), north easterly (17 %) and the north westerly winds (14 %) occurred less frequently. Current flow in either direction was found to last for no longer than ~2 weeks at a time as was observed in May 2006 (Fig. 3.8).

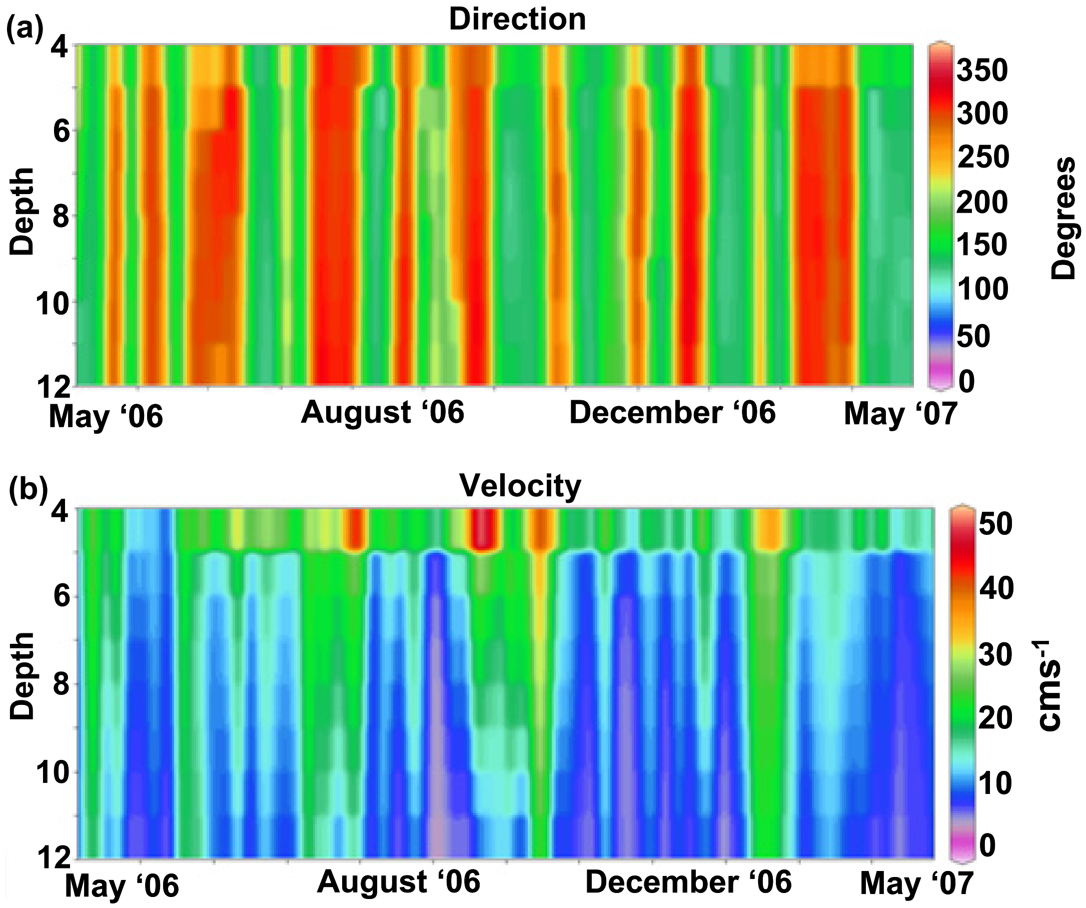


Figure 3.6: Direction (a) and velocity (b) during the twelve-month period (May 2006 – May 2007) using data collected from the bottom-moored ADCP on the 15 m depth contour in the shallow nearshore of eastern Algoa Bay. Figure supplied by Marine and Coastal Management, Cape Town South Africa

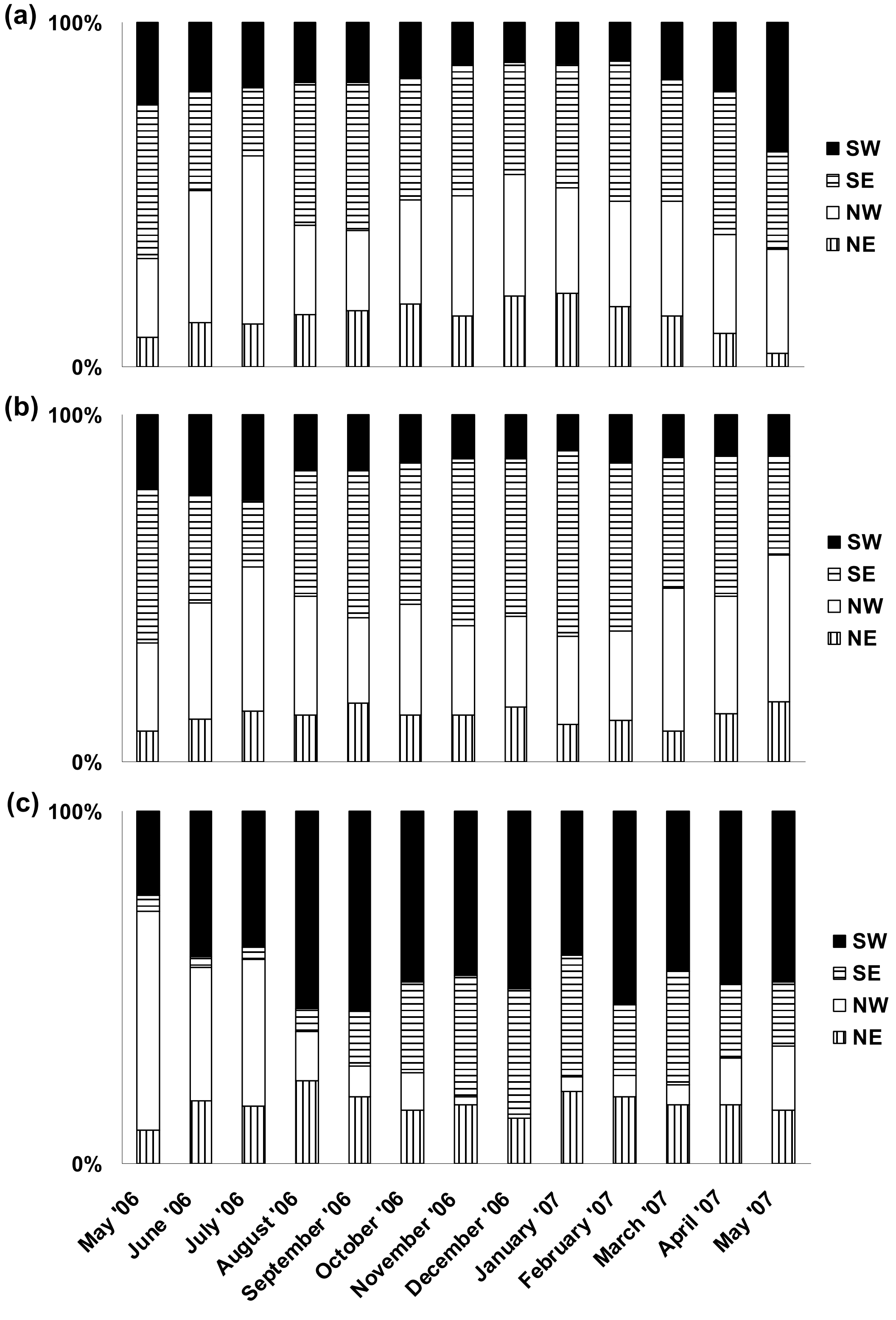


Figure 3.7: Direction of (a), near surface (4 m) currents (b), bottom (14 m) currents and (c), wind during the twelve-month period (May 2006 – May 2007) using data collected from the bottom-moored ADCP on the 15 m depth contour in the shallow nearshore of eastern Algoa Bay and from three weather stations around the Bay. Note that for wind, direction is from where the wind was blowing and for currents, direction is towards where the currents were flowing

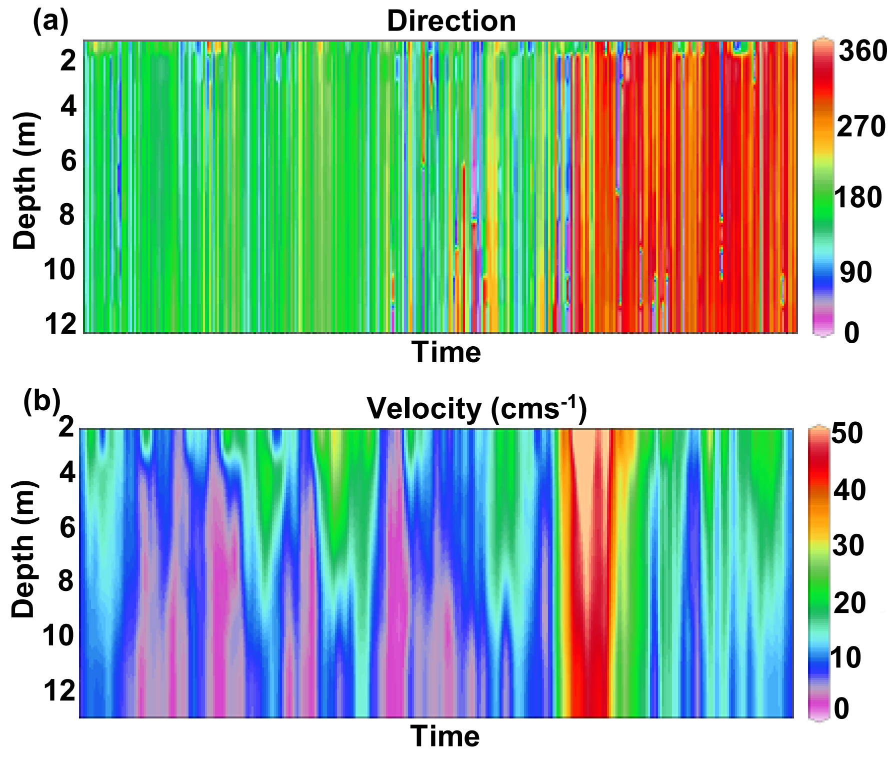


Figure 3.8: Characteristics of the shallow nearshore current environment during May 2007 using data collected from the bottom-moored ADCP on the 15 m depth contour in the shallow nearshore of eastern Algoa Bay. Figure supplied by Marine and Coastal Management

Current velocities in the region of the moored ADCP ranged between 0 – 149 cms^{-1}, with maximum velocity recorded in May 2007. The modal current velocity in the entire water column was 8 cms^{-1} (Fig. 3.9). Current velocities greater than 60 cms^{-1} did not feature notably in the shallow nearshore with percentage occurrences of <0.1 %. Current velocity was generally higher near the surface of the water column compared to the bottom (Fig. 3.10) with mean velocities decreasing from 29 cms^{-1} at a depth of 4 m to 11 cms^{-1} at 14 m. However, modal velocity near the surface of the water column was 8 cms^{-1} and 6 cms^{-1} at the bottom of the water column.

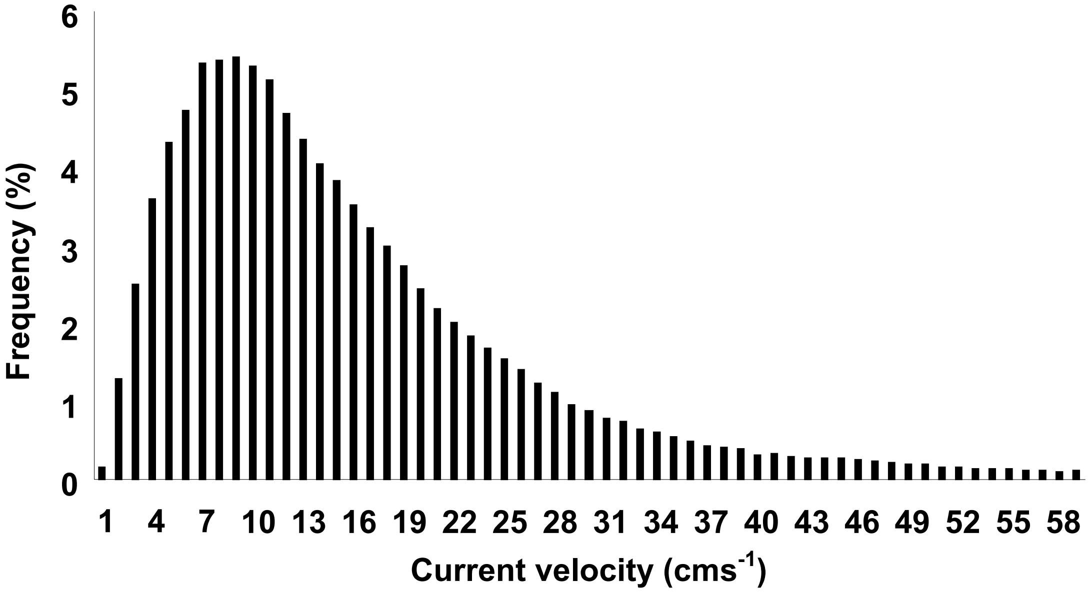


Figure 3.9: Frequency occurrence of current velocities during the twelve month sampling period (May 2006 – May 2007) using data collected from the bottom-moored ADCP on the 15 m depth contour in the shallow nearshore of eastern Algoa Bay

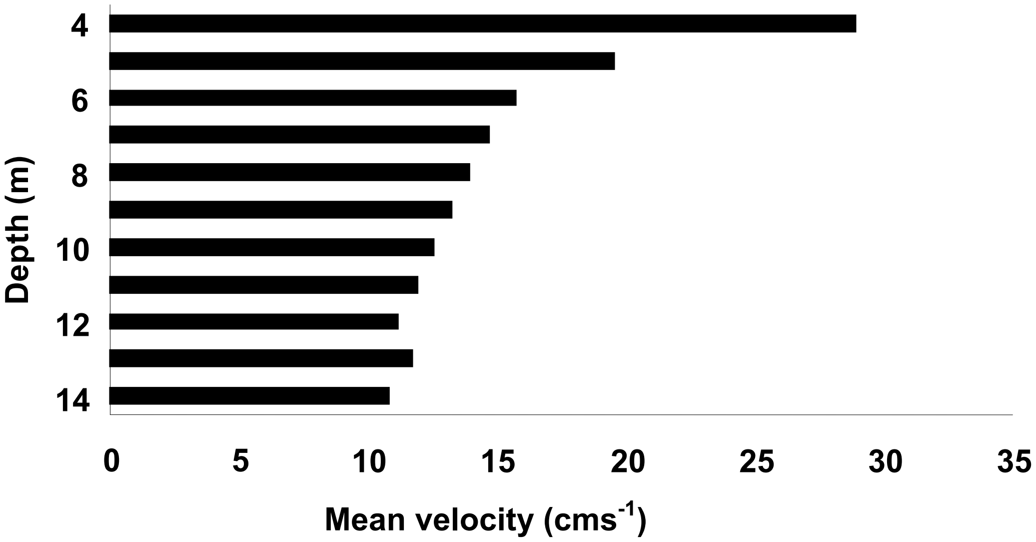


Figure 3.10: Mean velocity at each depth interval during the twelve month sampling period (May 2006 – May 2007) using data collected from the bottom-moored ADCP on the 15 m depth contour in the shallow nearshore of eastern Algoa Bay

4.3 Wind-correlation

A Pearson r correlation analysis between current direction near the surface (4 m) and wind direction measured at Bird Island, Coega and Port Elizabeth Harbour showed that the best correlation exists with no lag at Bird Island (Table 3.1). Current direction was negatively correlated with wind direction that occurred on the day at Bird Island. Current velocity near the surface (4 m) of the water column of the shallow nearshore was positively correlated with wind speed that occurred on the day at Port Elizabeth (Table 3.1).

Table 3.1: Correlations between current direction and velocity near the surface of the water column (4 m) with wind direction and speed, showing the correlation coefficient (r) and significant value (ns = not significant). Best fit is bolded

	Current Direction vs. Wind Direction		
Location	**Lag**	**r**	**P**
Coega	On the day	-0.33	<0.001
Coega	1 day earlier	-0.49	<0.001
Coega	2 days earlier	0.10	ns
Coega	3 days earlier	0.13	<0.05
Port Elizabeth	On the day	-0.49	<0.001
Port Elizabeth	1 day earlier	-0.18	<0.001
Port Elizabeth	2 days earlier	0.13	<0.05
Port Elizabeth	3 days earlier	0.08	ns
Bird Island	**On the day**	**-0.55**	**<0.001**
Bird Island	1 day earlier	-0.12	<0.05
Bird Island	2 days earlier	0.13	<0.05
Bird Island	3 days earlier	0.02	ns
	Current Velocity vs. Wind Speed		
Location	**Lag**	**r**	**P**
Coega	On the day	0.33	<0.001
Coega	1 day earlier	0.17	<0.01
Coega	2 days earlier	0.11	ns
Coega	3 days earlier	0.26	ns
Port Elizabeth	**On the day**	**0.49**	**<0.001**
Port Elizabeth	1 day earlier	0.29	<0.001
Port Elizabeth	2 days earlier	0.20	<0.001
Port Elizabeth	3 days earlier	0.14	<0.01
Bird Island	On the day	0.41	<0.001
Bird Island	1 day earlier	0.08	ns
Bird Island	2 days earlier	0.02	ns
Bird Island	3 days earlier	0.01	ns

The correlation analysis between current direction at the bottom of the water column (14 m) and wind direction measured at Bird Island, Coega and Port Elizabeth Harbour showed that the best correlation exists with no lag at Bird Island (Table 3.2). Current velocity at the bottom (14 m) of the water column was negatively correlated with wind speed at Port Elizabeth (Table 3.2). Equations of best fit are described in Table 3.3.

Table 3.2: Correlations between current direction and velocity at the bottom of the water column (14 m) with wind direction and speed, showing the correlation coefficient (r) and significant value (ns = not significant). Best fit is bolded

Current Direction vs. Wind Direction			
Location	**Lag**	**r**	**P**
Coega	On the day	0.10	ns
Coega	1 day earlier	0.12	<0.05
Coega	2 days earlier	-0.02	ns
Coega	3 days earlier	-0.06	ns
Port Elizabeth	On the day	0.15	<0.05
Port Elizabeth	1 day earlier	0.18	<0.001
Port Elizabeth	2 days earlier	-0.05	ns
Port Elizabeth	3 days earlier	-0.08	ns
Bird Island	**On the day**	**0.21**	**<0.01**
Bird Island	1 day earlier	0.13	<0.05
Bird Island	2 days earlier	-0.02	ns
Bird Island	3 days earlier	-0.06	ns

Current Velocity vs. Wind Speed			
Location	**Lag**	**r**	**P**
Coega	On the day	-0.21	<0.001
Coega	1 day earlier	-0.19	<0.001
Coega	2 days earlier	-0.15	ns
Coega	3 days earlier	0.01	ns
Port Elizabeth	**On the day**	**-0.34**	**<0.001**
Port Elizabeth	1 day earlier	-0.29	<0.001
Port Elizabeth	2 days earlier	0.02	ns
Port Elizabeth	3 days earlier	0.03	ns
Bird Island	On the day	-0.09	ns
Bird Island	1 day earlier	-0.14	<0.05
Bird Island	2 days earlier	0.01	ns
Bird Island	3 days earlier	0.10	ns

Table 3.3: Best fit equations for relationships between current direction with wind direction, and current velocity with wind speed

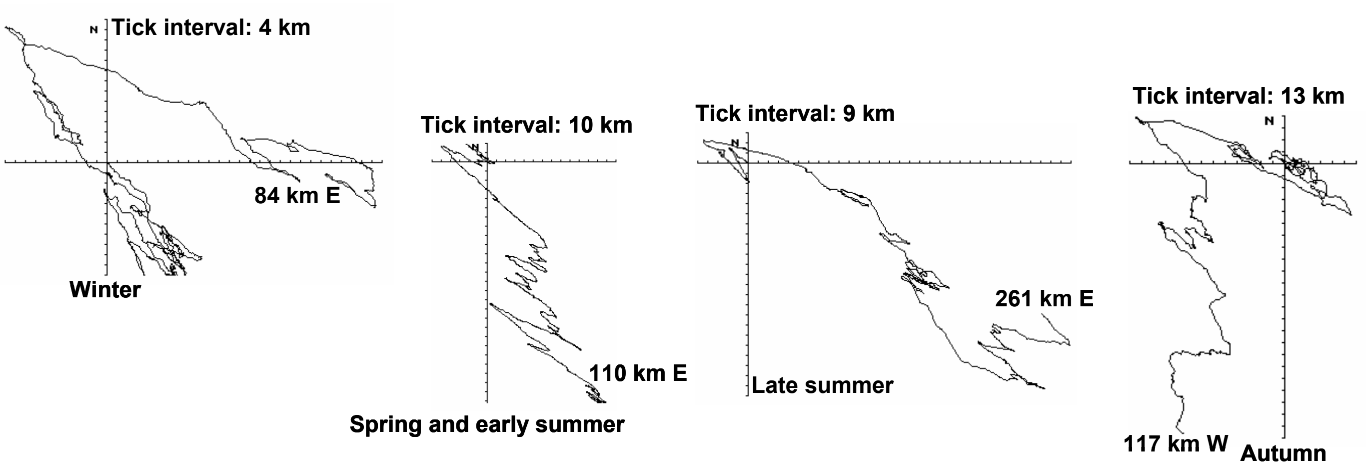
Location	Lag	Best Fit Equation
	Current Direction vs. Wind Direction (4 m)	
Bird Island	On the day	330.71 – 0.79 (Current Direction)
	Current Velocity vs. Wind Speed (4 m)	
Port Elizabeth	On the day	2.60 + 0.08 (Current Velocity)
	Current Direction vs. Wind Direction (14 m)	
Bird Island	On the day	155.00 + 3.50 (Current Direction)
	Current Velocity vs. Wind Speed (14 m)	
Port Elizabeth	On the day	7.40 – 0.01 (Current Velocity)

4.4 Passive particle transport

Total progressive displacement plots (Fig. 3.11) provide an indication of the potential transport of passive eggs and preflexion larvae. These plots highlight changes that occur at both the seasonal and depth level. Approximately every three months, data was retrieved from the moored ADCP and stored on a hard drive by Marine and Coastal Management. The ADCP memory was then cleared to record the next three months worth of oceanographic data. The seasonal plots in this study were grouped according to these time intervals. Data from the moored ADCP was grouped into winter (May 2006 – August 2006), spring and early summer (August 2006 – December 2006), late summer (December 2006 – March 2007) and autumn (March 2007 – May 2007) groupings and near surface (4 m) and bottom (14 m) categories and plotted accordingly (Fig 3.11).

It is important to note that the scale along the west-east axis is different for each season plotted in Figure 3.11. Displacement in both the near surface and bottom layers was similar in direction for all seasons. During winter (May 2006 – August 2006), near surface and bottom eggs and preflexion larvae released from the moored ADCP at the centre of the study area would have a net displacement of 84 km east and 24 km east respectively. During spring and early summer (August 2006 – December 2006) net displacement from the ADCP was 110 km near the surface and 186 km at the bottom of the water column. Greatest net displacement was observed during late summer (December 2006 – March 2007) with a net displacement from the origin of 261 km near the surface and 270 km at the bottom of the water column. During autumn (March 2007 – May 2007) net displacement from the origin was 117 km west in the near surface and 37 km west at the bottom of the water column.

(a) Near surface (4 m)



(b) Bottom (14 m)

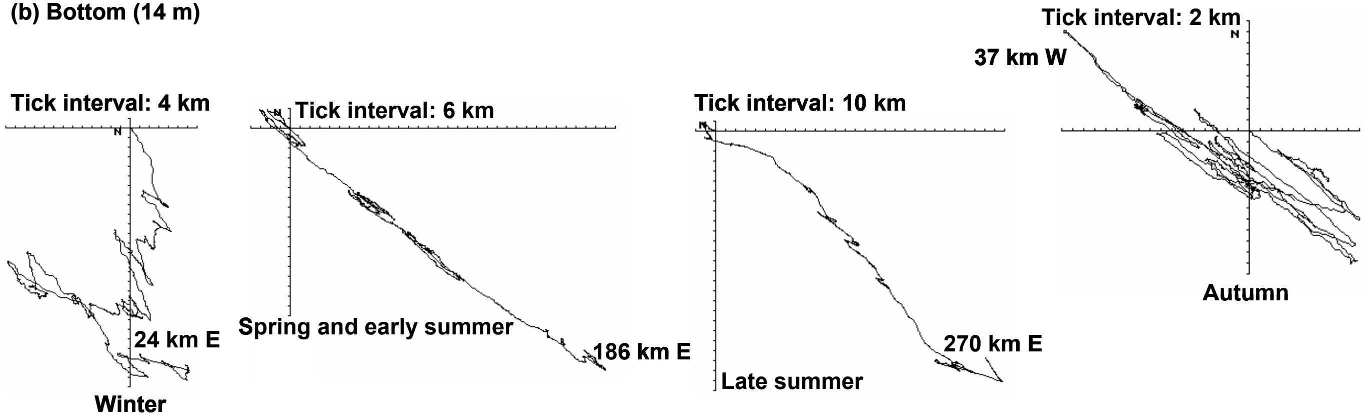


Figure 3.11: Progressive vector plots for the (a) near surface and (b) bottom of the water column during the twelve month sampling period (May 2006 – May 2007) using data collected from the bottom-moored ADCP on the 15 m depth contour in the shallow nearshore of eastern Algoa Bay. The twelve month sampling period has been divided equally into four seasonal components each of a three month duration. For each season a net displacement from the origin of the ADCP is given. Figure supplied by Marine and Coastal Management

DISCUSSION

5.1 One-day profiling surveys: current direction and velocity

Data collected from the one-day ADCP surveys indicated three different flow patterns exist in the shallow nearshore region of eastern Algoa Bay (eastward, westward and mixed). The presence of both eastward and westward flows that are uni-directional throughout the water column are indicative of alongshore currents in the bay. Roberts (1990) suggested that nearshore currents within the western bight of Algoa Bay are primarily driven by four prominent winds within the region (i.e. SW, ENE, NW and SSE), which set up distinct circulation patterns. The correlations between current direction and velocity with wind obtained in this study indicate that the shallow nearshore currents in the eastern sector of Algoa Bay are also influenced to a degree by wind as observed by Roberts (1990). Stronger correlations near the surface of the water column indicate that wind significantly influences currents near the surface, with a weaker correlation occurring between wind and currents near the bottom of the water column. With an increase in the lag period, correlation near the surface of the water column decreases and near the bottom of the water column correlation sometimes weakens with lag and breaks down completely. However, the lack of high correlation coefficient values suggests that wind is not the only driving force. Other factors including temperature, salinity, depth contours, tide and the shoreline could influence ocean current velocities and direction (Gill and Niller, 1973; Johnson and Willmott, 1981). Prevailing wind influences the direction of surface currents very quickly. Roberts (1990) noted that strong winds are capable of influencing the direction of bottom layers of the water column. Lighter winds will only influence the direction of currents in the surface layers of the water column. Residual bottom currents generated by past strong winds and surface currents induced by present winds can cause complex multidirectional current profiles (Roberts, 1990). Similarly, mixed current flow throughout the water column observed in this study could be an indication of this reflective wind influence.

5.2 Moored ADCP survey: current direction

The moored ADCP data showed four distinct current patterns in the shallow nearshore of the eastern sector of Algoa Bay. At the near surface and the bottom of the water column, the offshore flowing south eastward and to a slightly lesser extent the onshore flowing north westward current occurred most frequently during the study period. A previous study noted that the eastward direction of flow very close to the coast often reflects wind-forcing and swell angle (Schumann et al., 1982). The eastward flow observed here was also noted by Boyd et al. (1992) who showed a similar alongshore flow confined close inshore at Port Elizabeth. Boyd et al. (1992) suggested that the eastward velocities characterising these inshore coastal currents are significantly faster than the westward advection of the Agulhas Current. The presence of both eastward and westward flow in the present study suggests that although the inshore return tongues influence the eastward direction of shallow nearshore currents in the eastern sector of Algoa Bay, the Agulhas Current will occasionally create a net westward movement of water.

In the Tsitsikamma National Park, some 150 km west of Algoa Bay, the eastward current dominated (68 %) over the westward flow (32 %) indicating the presence of a semi-permanent alongshore current (Roberts and van den Berg, 2005). The general eastward displacement observed by Tilney et al. (1996) and Roberts and van den Berg (2005) in the Tsitsikamma was also evident in Algoa Bay. Tilney et al. (1996) and Roberts and van den Berg (2005) observed periods of sustained eastward flow lasting ~4 weeks, with the westward current being of a shorter duration within the Park. In the present study however, sustained eastward or westward flow would last no longer than ~2 weeks at any one time during the study period.

5.3 Moored ADCP survey: current velocity

A mean current velocity of 18 cms^{-1}, across all depths and over the entire sampling period (May 2006 – May 2007), was recorded from the moored ADCP in the eastern sector of Algoa Bay. Currents close to the coast in the western sector of Algoa Bay however are known to be very slow with mean velocities not exceeding 10 cms^{-1}, however anomalies where velocities in excess of 20 cms^{-1} have been recorded (Schumann et al., 2005). The western sector of Algoa Bay is protected from wave action and the major influence of the Agulhas Current (Schumann et al., 2005) by Cape Recife. In addition, slow velocities experienced in the nearshore waters of the western sector could be a result of increased bottom friction and reduced wind shear in the lee of the coast (Roberts, 1990). In the exposed eastern sector of Algoa Bay, the influence of the swell and wind fetch could result in greater current velocities. A maximum velocity of 149 cms^{-1} was recorded in the present study. A maximum velocity of 115 cms^{-1} was recorded in the shallow nearshore of the Tsitsikamma National Park further south along the coast (Roberts and van den Berg, 2005). However, when ADCP data in this study were averaged for the surface layers, similar mean velocities ranging from 23 – 29 cms^{-1} (Attwood et al., 2002; Roberts and van den Berg, 2005) were observed for this temperate coastal region. Generally, velocity decreased with depth with a speed of ~29 cms^{-1} recorded at a depth of 4 m decreasing to ~11 cms^{-1} at a depth of 14 m. In the Tsitsikamma nearshore, a similar trend is observed with current velocity decreasing from ~25 cms^{-1} at the surface of the water column to a mean of ~10 cms^{-1} recorded at 31 m (Roberts and van den Berg, 2005). A modal velocity of only 8 cms^{-1} and 6 cms^{-1} were recorded in the near surface (4 m) and bottom (14 m) of the water column respectively in the study area.

5.4 Egg and larval fish transport

An average current velocity of ~29 cms^{-1} recorded in this study at a depth of 4m translates to a rate of travel of 25.1 km day^{-1} for a passive particle within the water column. Similarly an average velocity of 11 $cm.s^{-1}$ recorded at a depth of 14 m translates to a rate of travel of 9.5 km day^{-1}. However, modal speeds are probably a more accurate reflection of transport in the bay. A modal current velocity of 8 $cm.s^{-1}$ at the near surface (4 m) translates to a rate of travel of only 6.9 km day^{-1}, and a modal current velocity of 6 cms^{-1} at the bottom of the water column (14 m) will only travel 5.2 km day^{-1}. When considering modal speeds in conjunction with current direction, a totally different dispersal effect is observed. The fact that no particular currents in the bay flow for longer than 2 weeks, we can recalculate trajectories and get a totally different and somewhat smaller dispersal effect than that predicted by other local studies (Tilney et al., 1996; Attwood et al., 2002; Roberts and van den Berg, 2005). The maximum dispersal larvae can therefore undergo in any one direction within Algoa Bay is ~95 km in the near surface and ~70 km at the bottom of the water column before wind-forced current direction and velocity changes occur. Ultimately progressive vector plots enable net displacement to be calculated a little more accurately using actual data.

The progressive vector plots indicate a theoretical transport of eggs and preflexion larvae in an easterly direction in winter, spring and summer and a westerly direction in autumn. These results are similar to those recorded further south in the

Tsitsikamma National Park (Roberts and van den Berg, 2005). However, the magnitude of the displacement observed in the Tsitsikamma National Park (Roberts and van den Berg, 2005) is three fold greater than that observed in the present study. This is probably due to Tsitsikamma being an exposed, open coastline whereas Algoa Bay is more sheltered.

In summer, the south eastward current dominates flow in the study area and vector plots of passive transport support the movement of eggs and preflexion larvae in an eastward direction. This is advantageous for fishes during peak spawning along the Eastern Cape coast in spring and summer as net movement is towards warmer water up the coast, limiting the loss of eggs and larvae to cool temperate waters in the west. Pelagic larval duration will also be shorter in warmer water and this in turn will reduce exposure to planktonic predators and thus mortality (Bailey and Houde, 1989; Ferron and Leggett, 1994; Green and Fisher, 2004). Furthermore, in spring and summer during the main spawning season of many fish species (Heemstra and Heemstra, 2004), greater net displacement was observed in the bottom of the water column than that observed near the surface. In spring and early summer, distances of 186 km east at the bottom of the water column place propagules near Kidds Beach (33°05'31"S, 27°48'26"E), south of the city of East London and in late summer, distances of 270 km east at the bottom of the water column place propagules near the Kei River Mouth (32°35'53"S, 28°30'43"E), north of East London. This bottom displacement is effective in dispersing bottom eggs during the main spawning season in Algoa Bay. This has important implications in the placement of neighbouring marine protected areas. However, for the rest of the year, bottom dispersal is minimal leading to possible entrainment of bottom eggs in the bay. These results should however be regarded with caution as the eggs of many taxa don’t necessarily remain near the bottom of the water column.

During May 2007, the north westward current tended to dominate flow, creating the westward transport of eggs and preflexion larvae observed in autumn (March 2007 – May 2007). However, the northerly component introduces a shoreward component to westward flow. North westward currents dominated flow in the winter months of June 2006 and July 2006. Net transport of eggs and preflexion larvae was however east during this winter period (May 2006 – August 2006), probably due to reflection off the coast in the south south-east facing bay. The magnitude of the net displacement of passive particles in the water column, 84 km east near the surface and 24 km east at the bottom of the water column, observed during this winter period (May 2006 – August 2006) was however less than that observed during the summer period when displacement reached up to 261 km east near the surface and 270 km at the bottom of the water column.

Investigations of currents and the dispersal of passive eggs and preflexion larvae originating within Tsitsikamma National Park all suggest that these propagules will be dispersed beyond the boundaries reseeding adjacent fished areas with larval recruits (Tilney et al., 1996; Attwood et al., 2002; Roberts and van den Berg, 2005). Attwood et al. (2002) concluded that planktonic organisms have the potential to be transported beyond the Tsitsikamma National Park boundaries (70 km east to west by 5.6 km north to south) within 48 hours (Attwood et al., 2002). Roberts and van den Berg (2005) suggested that larvae in the surface of the water column can theoretically be dispersed from the middle of the park to distances exceeding 220 km per month. However, dispersal in Algoa Bay is far less which would lead to localized entrainment of eggs and early larvae within the area.

Measurements from vector plots presented here should however be regarded with caution as the displacement observed does not take into account factors such as bathymetry or coastline features which can create large deviations from that observed here (Roberts and van den Berg, 2005; van der Molen et al., 2007). Particular bathymetry and coastline features within Algoa Bay all create barriers to continuous flow. The bay is straddled between two rocky headlands, namely Cape Recife on the western boarder and Woody Cape on the eastern border. Other topographical features within the bay include Bird Island and a triad of small islands off the Coega River mouth. Furthermore the ADCP is fixed spatially and does not represent currents which occur adjacent to the ADCP. The vector plots in the present study also assume that particles remain at a constant depth near the surface and at the bottom of the water column which is not a realistic representation of larval fish movement. These plots are therefore overestimates of potential particle drift.

The prediction of larval dispersal is further complicated by larval fish behaviour. Studies have shown that larvae have sensory and swimming abilities that can strongly influence their net dispersal trajectories (Leis, 2003). The need therefore arises to combine oceanographic surveys with knowledge of larval fish behaviour in order to determine appropriate models of larval dispersal. The displacement observed in the progressive vector plots is over long time periods (three months). Larval fishes however usually have a short preflexion period (prior to caudal fin development) of less than one month (Leis, 2003). In the present study, coastal species that produce benthic eggs dominate catches within the proposed MPA (Chapter 2). These larvae will develop quicker as they are generally larger and have better developed sensory and swimming abilities than larvae from pelagic eggs and will therefore not be transported as far from shore (Leis, 1993; Leis, 1994). Nearshore coastal waters of Algoa Bay will experience average summer sea temperatures of ~21 °C (Chapter 2). Larvae from warmer waters will have shorter planktonic stages also limiting dispersal prior to the development of swimming abilities (Green and Fisher, 2004). A high degree of self-recruitment is known to occur in coral reef fish populations (Swearer et al., 1999; Jones et al., 1999). It has been suggested that self-recruitment in marine fish populations may be common and take place over much smaller scales (Almany et al., 2007) further limiting dispersal of larvae. This is highly probable in warm temperate waters where many adult fish species are highly resident (Brouwer et al., 2003). Postflexion and settlement stages of most larvae are capable of considerable swimming speeds (some exceeding 60 cms^{-1}) greater than local current regimes and endurance abilities (covering distances of over 100 kms) that can greatly influence their dispersal (Stobutzki and Bellwood, 1994; Leis et al., 1996; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997; Fisher et al., 2000; Bellwood and Fisher, 2001). Most larval stages can use vertical migration to avoid predators and to occupy different depths within the water column in search of favourable current regimes (Melville-Smith et al., 1981; Leis, 1986; Neilson and Perry, 1990; Leis, 1991; Leis and Carson-Ewart, 2000). Highly resident sparid larvae contribute notably to catches in the shallow nearshore of Algoa Bay (Chapter 2). Furthermore, the swimming abilities of certain Sparidae larvae from South African temperate waters (Chapter 4) are known to exceed current velocities observed in the present study. Studies have shown that larvae can control the direction of swimming to target nursery habitats (Leis, 2006; Leis et al., 2007). Larvae can also use sounds that originate from organisms such as snapping shrimp, fish and urchins on rocky and coral reefs as a cue to locate reefs (Tolimieri et al., 2000). Studies also suggest that the early stages of larvae may imprint to reef odour therefore facilitating retention or navigation towards natal reefs (Atema et al., 2002).

The elucidation of sensory and swimming abilities in fish larvae shows that dispersal cannot be predicted accurately and postflexion larvae will not follow passive transport trajectories. Models are at best limited to fish eggs and preflexion larvae. However dispersal is important in understanding connectivity in marine populations, which in turn is important in the effective management and conservation of marine populations (Palumbi, 2003). An understanding of larval fish behaviour and development will allow for more accurate models of larval dispersal and transport to be made. As larval dispersal determines connectivity in marine populations, revised models of larval dispersal will have implications for the design, frequency of placement and ultimately the efficacy of marine protected areas (Cowen et al., 2000; Leis, 2003).

6. CONCLUSION

Coastal habitats have distinctly different environmental characteristics and particular environmental drivers which include: the prevalence of wind, current velocities, direction and anomalies, weather and climate patterns which all govern dispersal or retention of eggs and fish larvae (Norcross and Shaw, 1984; Patterson and Swearer, 2007). Aspects such as spawning locations of fish populations, local oceanography, dominant winds, larval fish behaviour and conditions conducive to the survival of larvae will ensure that informed decisions are made when planning fish management tools such as MPAs and ultimately when managing and conserving fish populations (Mora and Sale, 2002). The results observed from this study and resultant predictions of larval transport cannot necessarily be applied to other areas along the South African coastline. However the drivers of coastal processes are similar and need to be assessed for specific coastal habitats or regions before management of fish populations via the entire life cycle can be achieved.

7. ACKNOWLEDGEMENTS

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8. REFERENCES CITED

ALMANY, G.R., BERUMEN, L.M., THORROLD, S.R., PLANES, S., JONES, G.P. 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* **316**: 742-744.

ATEMA, J., KINGSFORD, M.J., GERLACH, G. 2002. Larval reef fish could use odour for detection, retention and orientation to reefs. *Marine Ecology Progress Series* **241**: 151-160.

ATTWOOD, C.G., ALLEN, J., CLAASEN, P.J. 2002. Nearshore surface current patterns in the Tsitsikamma National Park, South Africa. *South African Journal of Marine Science* **24**: 151-160.

BAILEY, K.M., HOUDE, E.D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* **26**: 1-83.

BECKLEY, L.E. 1983. Sea-surface temperature variability around Cape Recife, South Africa. *South African Journal of Science* **79**: 436-438.

BECKLEY, L.E. 1986. The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. *South African Journal of Zoology* **21**: 244-252.

BECKLEY, L.E. 1988. Spatial and temporal variability in sea temperatures in Algoa Bay, South Africa. *South African Journal of Science* **84**: 67-69.

BELLWOOD, D.R., FISHER, R. 2001. Relative swimming speeds in reef fish larvae. *Marine Ecology Progress Series* **211**: 299-303.

BOEHLERT, G.W., MUNDY, B.C. 1988. Roles of behaviour and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* **3**: 51-67.

BORGES, R., BEN-HAMADOU, R., ALEXANDRA CHÍCHARO, M., RÉ, P., GONÇALVES, E.J. 2007. Horizontal spatial and temporal distribution patterns of nearshore larval fish assemblages at a temperate rocky shore. *Estuarine, Coastal and Shelf Science* **71**: 412-428.

BOYD, A.J., OBERHOLSTER, G.P.J. 1994. Currents off the west and south coasts of South Africa. *South African Shipping News and Fishing Industry* September/October: 26-28.

BOYD, A.J., TAUNTON-CLARK, J., OBERHOLSTER, G.P.J. 1992. Spatial features of the near-surface and midwater circulation patterns off western and southern South African and their role in the life histories of various commercially fished species. *South African Journal of Marine Science* **12**: 189-206.

BROUWER, S.L., GRIFFITHS, M.H., ROBERTS, M.J. 2003. Adult movement and larval dispersal of *Argyrozona argyrozona* (Pisces: Sparidae) from a temperate marine protected area. *African Journal of Marine Science* **25**: 395-402.

CHUTE, A.S., TURNER, J.T. 2001. Plankton studies in Buzzards Bay, Massachusetts, USA.V. Ichthyoplankton, 1987 to 1993. *Marine Ecology Progress Series* **224**: 45-54.

COWEN, R.K., LWIZA, K.M.M., SPONAUGLE, S., PARIS, C.B., OLSON, D.B. 2000. Connectivity of marine populations: open or closed? *Science* **287**: 857-859.

CSIR 1970. Algoa Bay coastal erosion investigation. Parts I and II. Hydraulic Research Unit, NMERI, CSIR, Stellenbosch, MEG 913 and 914.

FERRON, A., LEGGETT, W.C. 1994. An appraisal of condition measures for marine fish larvae. *Advances in Marine Biology* **30**: 217-303.

FISHER, R., BELLWOOD, D.R., JOB, S.D. 2000. Development of swimming abilities in reef fish larvae. *Marine Ecology Progress Series* **202**: 163-173.

GILL, A.E., NILLER, P.P. 1973. The theory of the seasonal variability in the ocean. *Deep Sea Research* **20**: 141-177.

GORDON, L.R. 1996. Principles of operation for Acoustic Doppler Current Profilers. RD Instruments, San Diego, California 54 pp.

GOSCHEN, W.S., SCHUMANN, E.H. 1988. Ocean current and temperature structures in Algoa Bay and beyond in November 1986. *South African Journal of Marine Science* **7**: 101-116.

GOSCHEN, W.S., SCHUMANN, E.H. 1994. An Agulhas Current intrusion into Algoa Bay during August 1988. *South African Journal of Marine Science* **14**: 47-57.

GOSCHEN, W.S., SCHUMANN, E.H. 1995. Upwelling and the occurrence of cold water around Cape Recife, South Africa. *South African Journal of Marine Science* **16**: 57-67.

GREEN, B.S., FISHER, R. 2004. Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. *Journal of Experimental Marine Biology and Ecology* **299**: 115-132.

HARRIS, S.A., CYRUS, D.P., BECKLEY, L.E. 1999. The larval fish assemblage in the nearshore coastal waters off the St Lucia Estuary, South Africa. *Estuarine, Coastal and Shelf Science* **49**: 789-811.

HARRIS, T.F.W. 1978. Review of coastal currents in South African wasters. *South African National Scientific Programmes Report* **30**: 1-103.

HEEMSTRA, P.C., HEEMSTRA, E. 2004. Coastal fishes of Southern Africa. South African Institute for Aquatic Biodiversity and National Inquiry Service Centre, Grahamstown 488 pp.

HERNÁNDEZ-MIRANDA, E., PALMA, A.T., OJEDA, F.P. 2003. Larval fish assemblages in nearshore coastal waters off central Chile: temporal and spatial patterns. *Estuarine, Coastal and Shelf Science* **56**: 1075-1092.

JOHNSON, J.A., WILLMOTT, A.J. 1981. An unsteady wind-driven ocean circulation model. *Dynamics of Atmosphere and Oceans* **6**: 1-27.

JONES, G.P., MILICICH, M.J., EMSLIE, M.J., LUNOW, C. 1999. Self-recruitment in a coral reef fish population. *Nature* **402**: 802-804.

KINGSFORD, M.J., LEIS, J.M., SHANKS, A., LINDEMAN, K., MORGAN, S., PINEDA, J. 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* **70**: 309-340.

KINLAN, B.P., GAINES, S.D. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* **84**: 2007-2020.

LEIS, J.M. 1982. Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawaii. *Marine Biology* **72**: 89-97.

LEIS, J.M. 1986. Vertical and horizontal distribution of fish larvae near coral reefs at Lizard Island, Great Barrier Reef. *Marine Biology* **90**: 505-516.

LEIS, J.M. 1991. Vertical distribution of fish larvae in the Great Barrier Reef lagoon, Australia. *Marine Biology* **109**: 157-166.

LEIS, J.M. 1993. Larval fish assemblages near Indo-Pacific coral reefs. *Bulletin of Marine Science* **53**: 362-392.

LEIS, J.M. 1994. Coral sea atoll lagoons: closed nurseries for the larvae of a few coral reef fishes. *Bulletin of Marine Science* **54**: 206-227.

LEIS, J.M. 2003. What does the larval fish biology tell us about the design and efficacy of marine protected areas. Aquatic protected areas: What works best and how do we know? Australian Society for Fish Biology, North Beach, WA pp. 170-180,

LEIS, J.M. 2006. Are larvae of demersal fishes plankon or nekton? *Advances in Marine Biology* **51**: 59-141.

LEIS, J.M., CARSON-EWART, B.M. 1997. Swimming speeds of the late larvae of some coral reef fishes. *Marine Ecology Progress Series* **159**: 165-174.

LEIS, J.M., CARSON-EWART, B.M. 1998. Complex behaviour by coral-reef fish larvae in open water and near-reef pelagic environments. *Environmental Biology of Fishes* **53**: 259-266.

LEIS, J.M., CARSON-EWART, B.M. 1999. *In situ* swimming and settlement behaviour of larvae of an Indo-Pacific coral-reef fish, the coral trout (Pisces, Serranidae, *Plectropomus leopardus*). *Marine Biology* **134**: 51-64.

LEIS, J.M., CARSON-EWART, B.M. 2000. Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. *Coral Reefs* **19**: 247-257.

LEIS, J.M., CARSON-EWART, B.M. 2001. Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. *Coral Reefs* **19**: 247-257.

LEIS, J.M., GOLDMAN, B. 1983. Studies on the biology of larval fishes in the Lizard Island area, Northern Great Barrier Reef. Proceedings: Inaugural Great Barrier Reef Conference James Cooke University Press, Townsville 221-225.

LEIS, J.M., SWEATMAN, H.P.A., READER, S.E. 1996. What the pelagic stages of coral reef fishes are doing out in the blue water: daytime field observations of larval behaviour. *Marine and Freshwater Research* **47**: 401-411.

LEIS, J.M., WRIGHT, K.J., JOHNSON, R.N. 2007. Behaviour that influences dispersal and connectivity in the small, young larvae of a reef fish. *Marine Biology* **153**: 103-117.

LUTJEHARMS, J.R.E. 1981. Features of the southern Agulhas Current circulation from satellite remote sensing. *South African Journal of Science* **77**: 231-236.

LUTJEHARMS, J.R.E., BAIRD, D., HUNTER, I.T. 1986. Seeoppervlak dryfgedrag aan die Suid-Afrikaanse suidkus in 1979. *South African Journal of Science* **82**: 324-326.

MACKAS, D.L., DENMAN, K.L., ABBOTT, M.R. 1985. Plankton patchiness: biology of the physical vernacular. *Bulletin of Marine Science* **37**: 652-674.

MELVILLE-SMITH, R., BAIRD, D., WOOLDRIDGE, T.H. 1981. The utilization of tidal currents by the larvae of an estuarine fish. *South African Journal of Zoology* **16**: 10-13.

MORA, C., SALE, P.F. 2002. Are populations of coral reef open or closed? *Trends in Ecology and Evolution* **17**: 422-428.

NEILSON, J.D., PERRY, R.I. 1990. Diel vertical migrations of juvenile fish: an obligate or facultative process? *Advances in Marine Biology* **106**: 115-168.

NORCROSS, B.L., SHAW, R.F. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. *Transactions of American Fisheries Society* **113**: 153-165.

PALOMERA, I., OLIVAR, M.P. 1996. Nearshore ichthyoplankton off the Costa Brava (northwest Mediterranean Sea). *Publicaciones Especiales de Instituto Español de Oceanografía* **22**: 71-75.

PALUMBI, S.R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* **13**: S146-S158.

PATTERSON, H.M., SWEARER, S.E. 2007. Long-distance dispersal and local retention of larvae as mechanisms of recruitment in an island population of a coral reef fish. *Austral Ecology* **32**: 122-130.

ROBERTS, M.J. 1990. Dispersion of a buoyant effluent discharged into the nearshore waters of Algoa Bay. M.Sc thesis 287 pp.

ROBERTS, M.J., VAN DEN BERG, M. 2005. Currents along the Tsitsikamma coast, South Africa, and potential transport of squid paralarvae and ichthyoplankton. *African Journal of Marine Science* **27**: 375-388.

SALE, P.F. 2004. Connectivity, recruitment variation, and the structure of reef fish communities. *Integrative and Comparative Biology* **44**: 390-399.

SCHUMANN, E.H. 1987. The coastal ocean off the east coast of South Africa. *Transactions of the Royal Society of South Africa* **46**: 215-228.

SCHUMANN, E.H. 1998. The coastal ocean off southeast Africa, including Madagascar. *The Sea* **11**: 557-582.

SCHUMANN, E.H., CHURCHILL, J.R.S., ZAAYMAN, H. 2005. Oceanic variability in the western sector of Algoa Bay, South Africa. *African Journal of Marine Science* **27**: 65-80.

SCHUMANN, E.H., MARTIN, J.A. 1991. Climatological aspects of the coastal windfield at Cape Town, Port Elizabeth and Durban. *South African Geographical Journal* **73**: 48-51.

SCHUMANN, E.H., PERRINS, L.-A., HUNTER, I.T. 1982. Upwelling along the south coast of the Cape Province, South Africa. *South African Journal of Science* **78**: 238-242.

SCHUMANN, E.H., ROSS, G.J.B., GOSCHEN, W.S. 1988. Cold water events in Algoa Bay and along the Cape south coast, South Africa, in March/April 1987. *South African Journal of Science* **84**: 579-583.

SPONAUGLE, S., COWEN, R.K. 1996. Nearshore patterns of coral reef fish larval supply to Barbados, West Indies. *Marine Ecology Progress Series* **133**: 13-28.

STOBUTZKI, I.C., BELLWOOD, D.R. 1994. An analysis of the sustained swimming abilities of pre- and post-settlement coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **175**: 275-286.

STOBUTZKI, I.C., BELLWOOD, D.R. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Marine Ecology Progress Series* **149**: 35-41.

SWEARER, S.E., CASELLE, J.E., LEA, D.W., WARNER, R.R. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* **402**: 799-802.

TILNEY, R.L., NELSON, G., RADLOFF, S.E., BUXTON, C.D. 1996. Ichthyoplankton distribution and dispersal in the Tsitsikamma National Park marine reserve, South Africa. *South African Journal of Marine Science* **17**: 1-14.

TOLIMIERI, N., JEFFS, A., MONTGOMERY, J.C. 2000. Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. *Marine Ecology Progress Series* **207**: 219-224.

VAN DER MOLEN, J., ROGERS, S.I., ELLIS, J.R., FOX, C.J., MCCLOGHRIE, P. 2007. Dispersal patterns of the eggs and larvae of spring-spawning fish in the Irish Sea, UK. *Journal of Sea Research* **58**: 313-330.

WATT-PRINGLE, P., STRYDOM, N.A. 2003. Habitat use by larval fishes in a temperate South African surf zone. *Estuarine Coastal and Shelf Science* **58**: 765-774.

WHITFIELD, A.K. 1998. Biology and ecology of fishes in South African Estuaries. Ichthyological Monographs of the JLB Smith Institute for Ichthyology, No. **2**: Grahamstown 232 pp.

CHAPTER 4

SWIMMING ABILITIES OF LATE STAGE LARVAE OF *DIPLODUS CAPENSIS* AND *SARPA SALPA* (PISCES: SPARIDAE) FROM THE TEMPERATE COASTAL WATERS OF THE EASTERN CAPE, SOUTH AFRICA

1. SYNOPSIS

Understanding the movement of marine fish larvae in coastal habitats requires an assessment of active swimming abilities. The critical speed (*U*-crit) and endurance swimming of late stage larvae of *Diplodus capensis* and *Sarpa salpa* (Family Sparidae), common inshore recreational linefish species, were measured in a laboratory swimming chamber. Postflexion and settlement stage larvae were collected from the wild in a small bay on the warm temperate coast of South Africa. Larvae were allowed to acclimate in captivity and tested soon after capture. For the endurance tests a speed of 18 cms^{-1} was selected as this approximated the mean current speed observed in the coastal environment of the area. The mean *U*-crit value (maximum swimming speed) for *D. capensis* (19 cms^{-1}) was similar to that of *S. salpa* (18 cms^{-1}), whereas mean endurance (km swum) was greater in *S. salpa* (8 km) than *D. capensis* (6 km). The increase in critical speed and endurance swimming abilities with standard length was best described by a linear relationship. At lengths between 12 – 15 mm BL, *D. capensis* was the better swimmer, whereas *S. salpa* was the better swimmer between 15 – 16 mm BL. Of all the larvae that swam at critical speed, 90 % were in an inertial environment. These swimming speeds exceed the modal current velocities observed in the shallow nearshore where these larvae occur abundantly, providing larvae with the potential to greatly alter their passive early stage, dispersal trajectories and ultimately influence their distribution in the nearshore.

2. INTRODUCTION

Most demersal teleost fishes have a pelagic larval stage (Moser et al., 1984; Leis, 1991). The larval stage underpins connectivity of fish populations on a geographical scale. Traditionally larvae were presumed to be distributed passively via ocean currents over large spatial scales until larvae settled into a suitable habitat (Frank et al., 1993; Roberts, 1997). This assumption does not take the behaviour of larval fishes into account but used hydrography to determine larval dispersal. Indeed, the larvae of most perciform fish have very limited swimming abilities during the preflexion stage. However, once the caudal fin has formed larvae of most species are capable of considerable swimming speeds (some exceeding 60 cms^{-1}) and endurance (covering distances of over 100 kms) (Stobutzki and Bellwood, 1994; Leis et al., 1996; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997b; Fisher et al., 2000; Bellwood and Fisher, 2001). These swimming abilities are important for the avoidance of predators, for locating food in the water column (Plaut, 2001) and for locating suitable settlement habitats (Stobutzki and Bellwood, 1997; Montgomery et al., 2001). Larval fish swimming experiments have proved the 'simplifying' assumption of passive transport invalid and the need therefore arises for a reassessment of the effect of larval fish behaviour on dispersal (Armsworth, 2000; Armsworth et al., 2001).

Early research on the swimming abilities of certain temperate marine larval fish described them as weak swimmers only capable of cruising speeds up to 5 cms^{-1} (Houde, 1969; Laurence, 1972; Westernhagen and Rosenthal, 1979; Blaxter, 1986; Miller et al., 1988; Jenkins and Welsford, 2002). However, these results have been disproved by recent research which has focused on larvae of temperate species belonging to Mullidae, Monocanthide, Scorpidae, (Dudley et al., 2000) Percichthyidae, Sciaenidae and Sparidae families (Trnski, 2002; Clarke et al., 2005; Leis et al., 2006). These larvae have swimming abilities comparable to those of tropical species which are capable of speeds up to 60 cms^{-1} (Stobutzki and Bellwood, 1994; Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997b; Stobutzki, 1998; Leis and Carson-Ewart, 1999; Leis and Stobutzki, 1999; Fisher et al., 2000; Fisher and Bellwood, 2001; Fisher and Bellwood, 2002; Fisher and Bellwood, 2003; Fisher, 2004; Fisher and Wilson, 2004; Fisher, 2005; Fisher et al., 2005). The differences in swimming performances of temperate and tropical species have been related to water temperature (Wardle, 1975; Wieser and Kaufmann, 1998). However, this variation can also be related to taxonomic differences and morphological development (Stobutzki and Bellwood, 1997; Leis and Carson-Ewart, 1997a; Stobutzki, 1998; Dudley et al., 2000). There is however, still ongoing debate whether the swimming abilities of reef fish larvae from tropical studies can (Dudley et al., 2000; Clarke et al.,

2005) or cannot (Stobutzki and Bellwood, 1994; Stobutzki and Bellwood, 1997) be related to that of temperate species.

Manipulative observations in the laboratory, where larvae are placed in experimental chambers and the current flow is controlled, is a methodology used in Australia and New Zealand to study the swimming abilities of larval fishes (Stobutzki and Bellwood, 1994; Stobutzki and Bellwood, 1997; Stobutzki, 1998; Dudley et al., 2000; Fisher and Bellwood, 2001; Fisher and Bellwood, 2002; Leis and Clarke, 2005; Leis, 2006). The *U*-crit method (Brett, 1964) measures the maximum aerobic swimming speed of larvae over a short period of time providing an estimate of the swimming capability or potential speed of larvae. The *U*-crit method is used for determining the potential small scale movement of larvae, both vertically to access different current regimes or to locate prey, and horizontally between different habitats at settlement (Fisher et al., 2000). This method also allows for comparisons between the critical speeds of larvae of different species and families. Many species have been found to be effective swimmers and are capable of speeds greater than that of the local current regimes in which they occur, and can therefore influence their dispersal trajectory (Fisher, 2005; Fisher et al., 2005).

Laboratory endurance testing methods, where larvae are swum without food or rest against a constant flow speed until they are unable to maintain position, are well known and provide vital information on how far larvae can swim (Stobutzki and Bellwood, 1997; Stobutzki, 1998; Dudley et al., 2000; Jenkins and Welsford, 2002; Fisher and Wilson, 2004). At a fixed speed, coral reef fish larvae have remarkable endurance abilities, capable of swimming for days and 100s of kms (Stobutzki and Bellwood, 1997). Larvae allowed to feed during endurance experiments have substantially greater endurance values (Fisher and Bellwood, 2001; Leis and Clarke, 2005). In the wild, food is readily available to larvae therefore the endurance estimates of unfed larvae are grossly underestimated (Leis and Carson-Ewart, 1998).

The study of larval fish swimming abilities is an important component in understanding larval fish dispersal patterns and recruitment success. Larvae that have control over their horizontal distribution in the water column can ultimately control their dispersal trajectories. A high degree of variation in the behaviour of larvae occurs among taxa and the exact extent to which these behaviours influence dispersal is unknown.

This study represents the first assessment of swimming abilities of larval fishes in South Africa. The aim of this study was to determine *U*-crit and endurance swimming abilities of late stage larvae of *Diplodus capensis* and *Sarpa salpa* (Sparidae). These two species are common inshore and are important recreational linefish species (Smith and Heemstra, 1995). Larvae of *D. capensis* and *S. salpa* are found abundantly in small rocky bays along the temperate coastline of South Africa (Strydom, in press). Morphological measurements of all larvae were made in order to determine any potential relationships with swimming abilities. Methodology has been standardized between Australian and South African research to allow for comparison of swimming abilities between temperate species in the family Sparidae

3. MATERIALS AND METHODS

3.1 Swimming chamber

A clear perspex swimming chamber (Fig. 4.1) with six lane-ways, based on the design by Stobutzki and Bellwood (1994) and modified by Clarke et al. (2005), was used to determine the critical speed and endurance swimming ability of the larvae. Each lane was 30 mm wide, 50 mm high and 180 mm long, with fine mesh covering the ends. A T-piece diffuser at the head of the chamber allowed for even distribution of flow. A 40 mm long section of flow straighteners, at the start of each lane-way, minimized turbulence within the chamber. Flow speeds within the chamber were controlled via a pre-calibrated valve. Flow rates were calibrated by recording the time taken for water flowing over the chamber's outlet weir to fill a container of known volume (2000 mL), divided by the cross-sectional area of the chamber (90 cm^2). At each angle of the valve the average of five calibrations was used for the flow speed. The system was recalibrated each time the chamber was set up. Flow speeds ranged from 1 – 36 cms^{-1}. The chamber design has negligible boundary layers (Stobutzki and Bellwood, 1997; Stobutzki, 1998; Fisher et al., 2000) with water velocity in the 5 mm closest to the wall not significantly different to that in the centre of the chamber (Stobutzki and Bellwood, 1997).

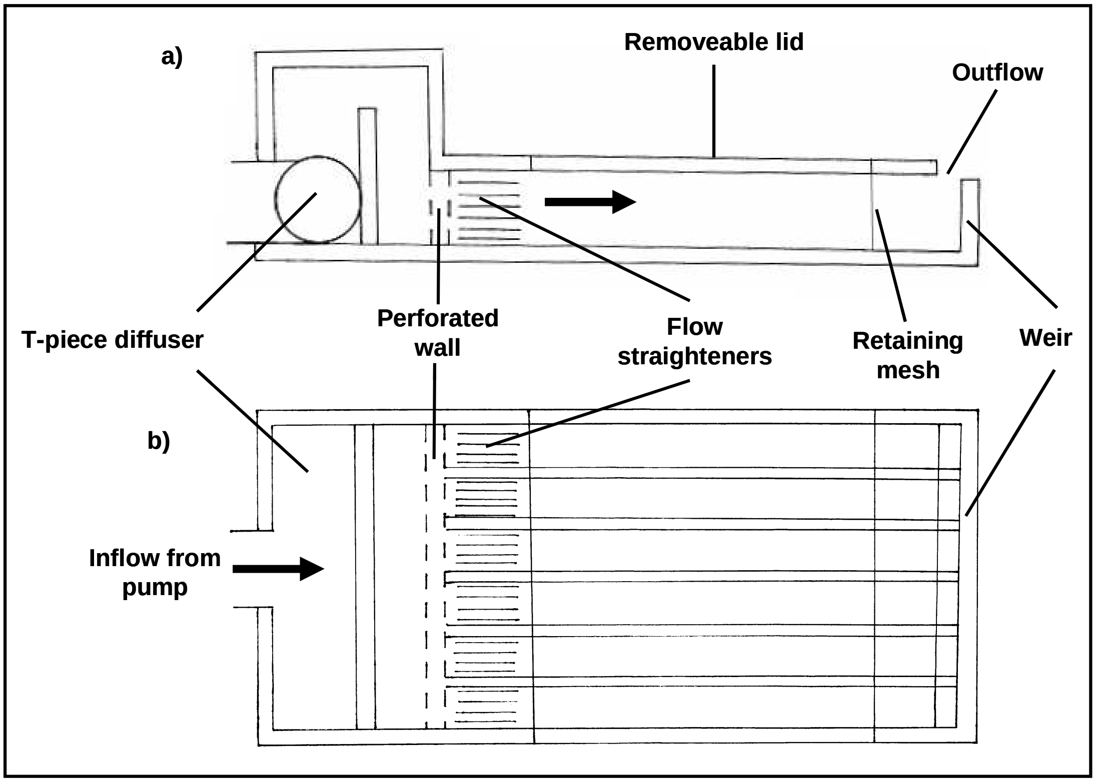

Figure 4.1: Schematic diagram of swimming chamber; a) side view and b) top view adapted from the design by Stobutzki and Bellwood (1997)

3.2 Larvae

Late-stage larvae (postflexion and settlement) of two important linefish species, *D. capensis* and *S. salpa*, belonging to the family Sparidae were studied. *Diplodus capensis* ranges from Angola to Mozambique and southern Madagascar (Smith and Heemstra, 1995). This marine inshore species favours turbulent waters and rocky shores. Juveniles utilize tidal pools, inshore reefs (Smale and Buxton, 1989) and the lower and middle reaches of certain warm temperate estuaries as nursery areas (Whitfield, 1998). A peak in spawning occurs from October – December in warm temperate areas of South Africa and from July – September in the subtropics (Coetzee, 1986). Adults attain a standard length of 45 cm and settles at a length of 18-22 mm (Heemstra and Heemstra, 2004). *Sarpa salpa* ranges from the Mediterranean and eastern Atlantic to southern Mozambique (Smith and Heemstra, 1995). Juveniles occur in warm-temperate estuaries, subtidal reefs, tidal pools and the sandy beach surf zone (Whitfield, 1998). Spawning occurs between April – September (Whitfield, 1998). Adults attain a standard length of 45 cm and settles at a length of 26-30 mm (Heemstra and Heemstra, 2004).

3.3 Larval fish collection

All larvae were collected using a larval seine net (Strydom, 2003) from Shark Bay, a small intertidal bay near Port Alfred (33°36' S, 26°54' E) that was 50 m wide and ~2 m deep. The catch was retained in white plastic buckets in fresh seawater and immediately transported (2 km) to the Port Alfred Marine Research Laboratory. Larvae were placed in aquaria with fresh flowing seawater and allowed to acclimate for 1 – 2 hours. All swimming experiments were conducted at ambient seawater temperatures at Port Alfred Marine Research Laboratory which ranged between 17 – 20 °C, with similar temperatures recorded in Shark Bay. All larvae showing signs of stress or damage were removed prior to experimentation.

3.4 Swimming methodology

Larvae were swum within 12 hours of capture using the swimming chamber. Larvae were randomly removed from the aquaria using a beaker and one larva was then placed into each lane-way of the chamber and was swum against a speed of 1 cms^{-1} for 8 – 10 mins to acclimate. Larvae showing signs of stress were removed. Two types of swimming experiments were conducted, namely a *U*-crit test which measures the maximum swimming speed of the larvae and an endurance test which measures the time and distance the larvae swim at one particular speed.

For *U*-crit tests, current speed starting at 1.5 cms^{-1} was increased by 2 cms^{-1} every 5 mins until larvae were unable to swim against the current. The time each larvae stopped swimming was recorded and *U*-crit was calculated using the equation by Brett (1964) cited in Clarke et al. (2005):

$$U\text{-crit} = U + (t/t_i \times U_i)$$

U = penultimate speed, U_i = speed increment (2 cms^{-1}), t = time swum at final speed, t_i = time increment (5min).

For the endurance tests, a constant flow speed of 18 cms^{-1} was selected. This speed was selected as it approximated the mean current speed in the shallow nearshore of the proposed Greater Addo Marine Reserve (Chapter 3). Larvae swam without food or rest until they were unable to swim against the current and came to rest against the downstream mesh in the raceway (Fig. 4.1). Measurements were made outdoors under shade with ambient light during the day and a fluorescent light was used for illumination at night. During the day, larvae were constantly observed and the exact time that larvae came to rest was recorded. During the night, larvae were observed every 3 hours and the time of rest was taken as the midpoint between when the larva was last seen swimming and when it was found no longer swimming. All larvae were collected after each trial and preserved in 70 % ethanol.

3.5 Morphological and meristic measurements

All larvae examined were in the postflexion or settlement stage of development. Larvae were cleared and stained in the laboratory. Morphological measurements included: body length BL (standard length), preanal length (PAL), body depth (BD), and head length (HL). Meristic counts included dorsal (D), anal (A) and caudal (C) fin rays and spines (where applicable).

3.6 Data analyses

Data were tested for normality and homogeneity of variance using a normal probability plot, Shapiro-Wilk test and Levene’s test and conformed to parametric assumptions. Critical swimming speed and endurance were regressed against all morphological variables measured to determine the best predictor of performance using linear, logarithmic, power and exponential models. The model with the greatest r^2 value was accepted. In the comparison between species, larvae were grouped by size into 1 mm increments. Differences in the mean *U*-crit and BL of the two species were examined using a t-test. For each species, best performers, which represented 25 – 35 % of the total number of individuals tested, were examined separately. Principal Component Analysis was used to determine if patterns exist between morphological and meristic measurements and the swimming abilities of larvae. Eigenvalues and eigenvectors were extracted from a correlation matrix. Reynolds number (Re) was calculated to determine in which hydrodynamic environment (viscous, intermediate or inertial) each larva was swimming in (Webb and Weihs, 1986). A viscous environment occurs when Re < 300, and an inertial environment occurs when Re > 1000 (Leis, 2003).

$$Re = U \times (L \div v)$$

L = body length (m), U = swimming speed (ms^{-1}) and v = kinematic viscosity of seawater at 20°C ($1.03 \times 10^{-6}\ m^2 s^{-1}$).

4. RESULTS

4.1 *U*-crit performance

Standard length provided a better fit for *U*-crit and endurance data than did the other morphological variables. The linear model provided the best fit (greatest r^2 values) and all equations are presented in Table 4.1.

U-crit increased with size and a linear model was the best representation of this increase for both *S. salpa* and *D. capensis* (Fig. 4.2). The fastest individual of *S. salpa* swam at a speed of 33.4 cms^{-1} at a settlement size of 21.3 mm which was the largest individual tested. However, the fastest individual of *D. capensis* was not the largest individual tested and swam at a speed of 35.2 cms^{-1} at a postflexion length of 13.5 mm. Critical speeds at any given size were 4.2 to 10.5 cms^{-1} faster for the best performers than for averaged larvae. The difference between best and averaged performers was 6 – 9.6 cms^{-1} for *D. capensis* and 4.2 – 10.5 cms^{-1} for *S. salpa*.

No significant difference in the mean *U*-crit (t-value = 18.0, P = 0.6) of the two species was observed, however *D. capensis* had a greater mean *U*-crit value (18.6 cms^{-1}) than *S. salpa* (18.0 cms^{-1}). A significant difference in standard length occurred between the two species (t-value = -20.4, P = 0.001). *S. salpa* larvae were larger with a mean standard length of 15.6 mm and *D. capensis* had a mean length of 11.6 mm (Table 4.2).

A significant positive correlation between *U*-crit in *S. salpa* and body length, preanal length, body depth and head length was observed, however no significant correlation between morphology and *U*-crit was observed in *D. capensis* (Table 4.3).

Table 4.1: Relationship between size (SL mm) and swimming performance for all larvae and best performers

			Critical speed (cms^{-1})				
Species	U-crit	All			Best		
	(cms^{-1} ± SD)	Equation	Size range (mm)	n	Equation	Size range (mm)	n
D. capensis	18.6 ± 7.7	1.05SL + 6.45, $r^2 = 0.03$, $P = 0.08$	9.7 – 16.0	94	0.91SL + 15.34, $r^2 = 0.11$, $P = 0.07$	9.7 – 15.4	29
S. salpa	18.0 ± 8.3	2.07SL – 14.14, $r^2=0.11$, $P < 0.005$	12.1 – 21.3	93	1.47SL + 3.42, $r^2 = 0.29$, $P < 0.005$	12.1 – 21.3	29
			Endurance (km)				
Species	Endurance	All			Best		
	(km ± SD)	Equation	Size range (mm)	n	Equation	Size range (mm)	n
D. capensis	5.9 ± 8.1	1.39SL – 8.94, $r^2=0.03$, $P = 0.22$	8.9 – 14.1	46	2.55SL - 10.87, $r^2 = 0.21$, $P = 0.11$	8.9 – 14.1	13
S. salpa	8.4 ± 15.2	3.86SL – 52.79, $r^2=0.18$, $P < 0.005$	12.2 – 19.0	50	8.04SL – 105.23, $r^2=0.62$, $P < 0.005$	12.2 – 18.6	12

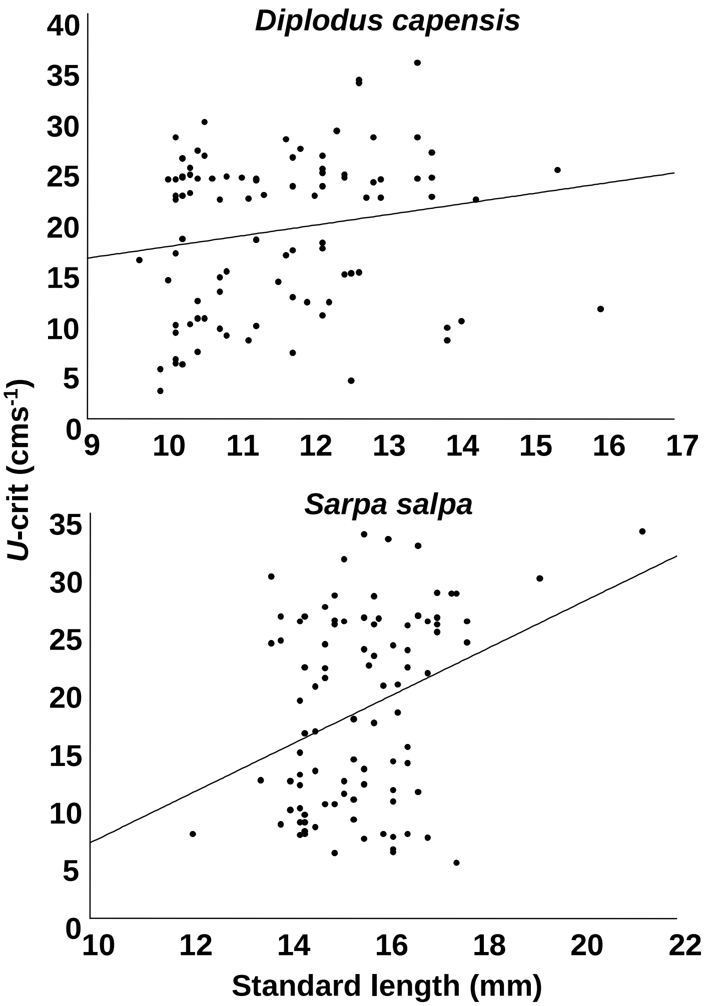

Figure 4.2: Critical swimming speed in warm temperate Sparidae, *Diplodus capensis* and *Sarpa salpa* measured in a laboratory swimming chamber at the Port Alfred marine laboratory

Table 4.2: Morphological and meristic mean values and ranges for *Diplodus capensis* and *Sarpa salpa* measured for the *U*-crit swimming test

	***U*-crit**			
	***Diplodus capensis* (n=94)**		***Sarpa salpa* (n=93)**	
	Mean	**Range**	**Mean**	**Range**
BL	11.6	9.7 – 16.0	15.6	12.1 – 21.3
PAL	6.7	4.8 – 10.0	9.4	6.9 – 14.1
BD	3.9	2.8 – 6.5	4.8	3.3 – 6.8
HL	4.0	2.4 – 6.0	5.4	3.9 – 7.4
D	XI, 14	X – XII; 11 – 15	X, 16	X – XI; 14 – 16
A	III,14	II – III; 12 – 15	III,14	II – III; 13 – 15
C	9 + 8	9 + 8	9 + 8	9 + 8

Table 4.3: Correlation between morphological measurements and *U*-crit values for *Diplodus capensis* and *Sarpa salpa*. r = correlation coefficient, p = p-value

	***U*-crit**	
	Diplodus capensis	***Sarpa salpa***
BL	r = 0.20, P = 0.08	r = 0.33, P < 0.001
PAL	r = 0.18, P = 0.05	r = 0.32, P < 0.01
BD	r = 0.13, P = 0.20	r = 0.21, P < 0.05
HL	r = 0.19, P = 0.07	r = 0.28, P < 0.01

4.2 Endurance performance

Endurance increased with size and a linear model was the best representation of this increase for both species (Fig. 4.3). The greatest distance swum was 64.8 km for *S. salpa* at a size of 18.6 mm and 32.4 km for *D. capensis* at a length of 9.8 mm, which were not the largest individuals tested. The endurance at any given size was 0.9 to 36 km further for the best performers than for averaged larvae. The difference between best and averaged performers was least for *D. capensis* (9.4 – 13 km) and greatest for *S. salpa* (0.9 – 36 km).

No significant difference in the mean endurance (t-value = -1.0, P = 0.3) abilities of the two species was observed. *Sarpa salpa* swam a greater mean distance (8.4 km) than *D. capensis* (5.9 km). A significant difference (t-value = -17.8, P = 0.001) in standard length was observed between the two species (Table 4.4), with *S. salpa* having a greater mean length (15.8 mm) than *D. capensis* (10.7 mm).

A significant positive correlation between endurance in *S. salpa* and body length, preanal length and head length was observed, however no significant correlation between morphology and *U*-crit was observed in *D. capensis* (Table 4.5).

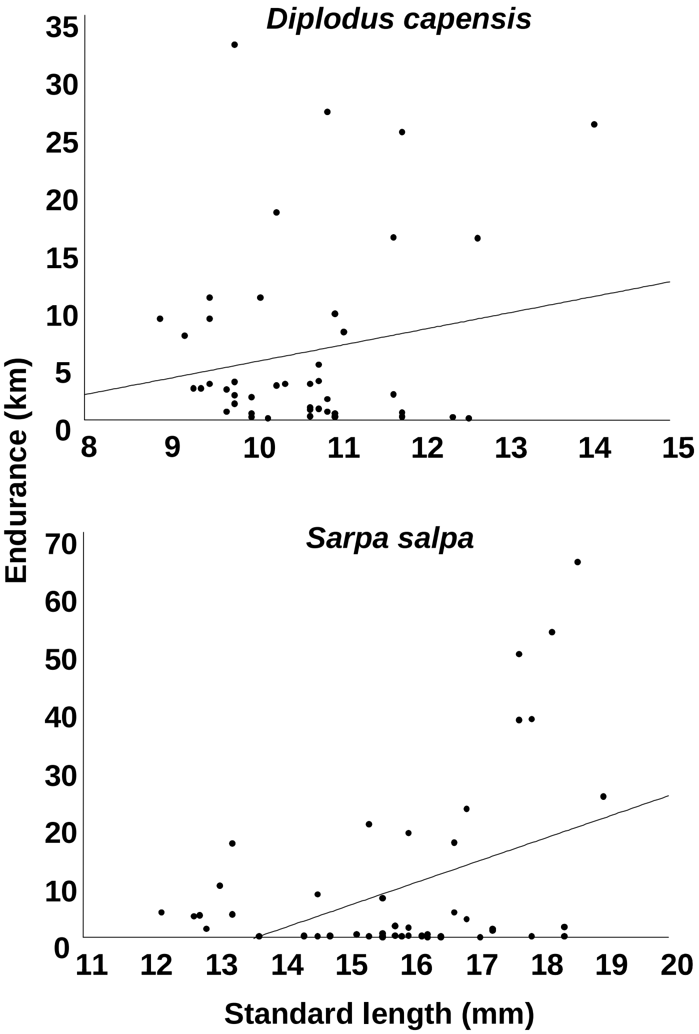

Figure 4.3: Endurance swimming in warm temperate Sparidae, *Diplodus capensis* and *Sarpa salpa* measured in a laboratory swimming chamber at the Port Alfred marine laboratory

Table 4.4: Morphological and meristic mean values and ranges for *Diplodus capensis* and *Sarpa salpa* measured for the endurance swimming test

	Endurance			
	***Diplodus capensis* (n=46)**		***Sarpa salpa* (n=50)**	
	Mean	**Range**	**Mean**	**Range**
BL	10.7	8.9 – 14.1	15.8	12.2 – 19.0
PAL	5.6	4.1 – 8.7	9.3	6.7 – 11.6
BD	3.2	2.2 – 4.4	4.6	3.5 – 6.1
HL	3.4	2.7 – 4.5	5.3	4 – 6.6
D	XI, 14	X – XII; 12 – 15	XI, 15	X – XI; 14 – 16
A	III,13	II – III; 12 – 14	III,14	II – III; 12 – 16
C	9 + 8	9 + 8	9 + 8	9 + 8

Table 4.5: Correlation between morphological measurements and endurance values for *Diplodus capensis* and *Sarpa salpa*. r = correlation coefficient, P = p-value

	Endurance	
	Diplodus capensis	***Sarpa salpa***
BL	r = 0.18, P = 0.22	r = 0.43, P < 0.01
PAL	r = 0.23, P = 0.13	r = 0.40, P < 0.01
BD	r = 0.09, P = 0.55	r = 0.28, P = 0.05
HL	r = 0.16, P = 0.29	r = 0.41, P < 0.01

4.3 Comparison between species

The mean swimming abilities over 1 mm size intervals were plotted for the comparison among species. Over the size range of 12 to 16 mm SL for which there was *U*-crit data for both species, *D. capensis* was initially the faster swimmer, with greater speeds observed for *S. salpa* at a size between 15 – 16 mm (Fig. 4.4). At lengths 12 – 13 mm, *D. capensis* was the faster swimmer by 13.8 cms^{-1}. A decrease in speed was observed for *D. capensis* in the 14 – 15 and 15 – 16 mm size category. In both species a general linear increase in critical speed with increasing standard length over the common size range was observed, with an increase of 0.1 to 3.7 cms^{-1} per mm standard length. *Diplodus capensis* had the slowest rate of increase whereas *S. salpa* had the fastest. Gaps in the data occur for *S. salpa* between size intervals of 18 – 19 and 20 – 21 mm as no larvae at these lengths were caught.

Mean endurance values increased from 8.8 km (8 – 9 mm BL) to 25.5 km (14 – 15 mm BL) for *D. capensis* (Fig. 4.5). Similarly for *S. salpa*, mean endurance values increased from 3.3 km (12 – 13 mm BL) to 28.8 km (18 – 19 mm BL). Over the size range of 12 – 15 mm BL for which there was endurance data for both species, *D. capensis* had the greatest endurance (2 – 24 km). Gaps in the data occur for *D. capensis* between the size interval of 13 – 14 mm as no larvae at these lengths were caught.

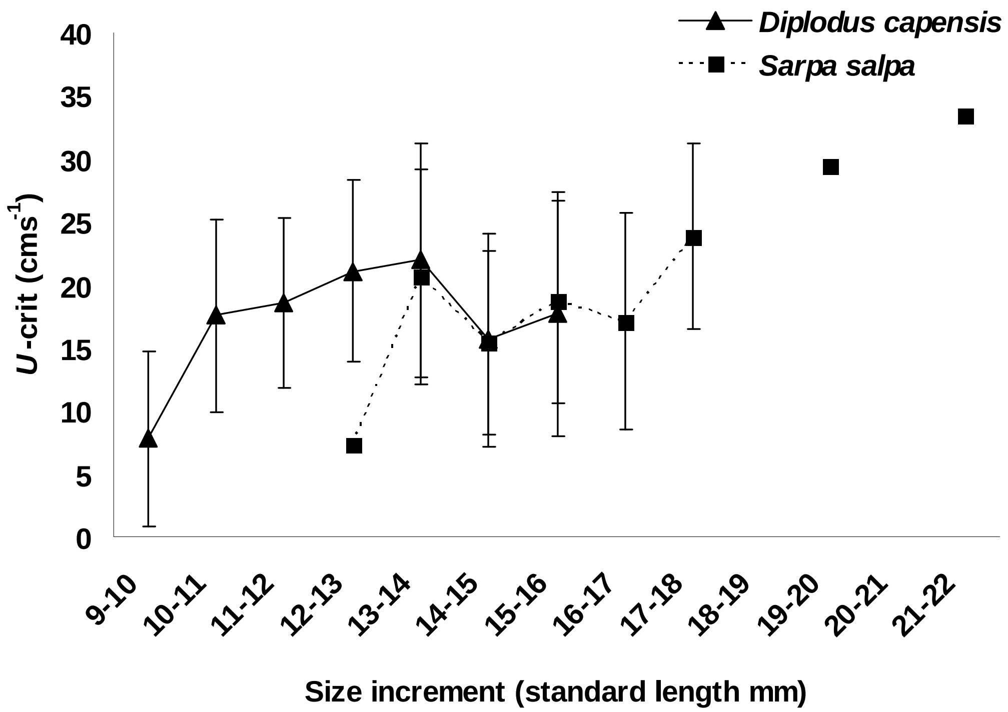

Figure 4.4: Critical swimming speed (*U*-crit) based on the mean performance in each 1 mm size increment showing standard deviation for *Diplodus capensis* and *Sarpa salpa*. Note: Gaps in the data for *S. salpa* between size intervals of 18 – 19 and 20 – 21 mm as no larvae at these lengths were caught

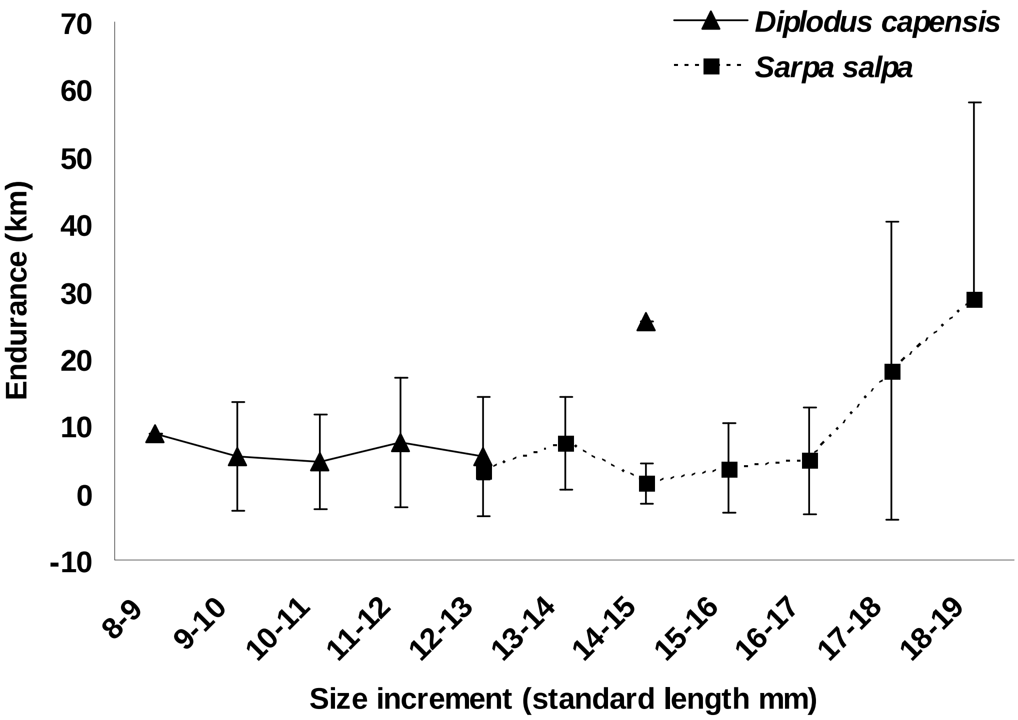

Figure 4.5: Endurance swimming based on mean performance in each 1 mm size increment showing standard deviation for *Diplodus capensis* and *Sarpa salpa*. Note: Gaps in the data for *D. capensis* between the size interval of 13 – 14 mm as no larvae at these lengths were caught

When the critical speed data were scaled to body length (BLs^{-1} based on SL), different results were observed for *S. salpa* and *D. capensis* (Table 4.6). An increase in scaled speed (BLs^{-1}) with standard length was observed in *S. salpa* but a weak decrease in scaled speed with increasing standard length was observed in *D. capensis*. A significant difference in the mean scaled speed (t-value = 5.28, p = 0.001) of the two species with a greater mean observed in *D. capensis* (16.1 BLs^{-1}) than *S. salpa* (11.5 BLs^{-1}). A significant positive correlation between scaled speed and *U*-crit was observed for both *D. capensis* ($r^2 = 0.92$, p = 0.001) and *S. salpa* ($r^2 = 0.95$, p = 0.001) (Fig. 4.6).

Table 4.6: Relationship between standard length (mm) and critical speed scaled as body lengths (BLs^{-1}) in *Diplodus capensis* and *Sarpa salpa*.

Species	Linear equation	P	r^2
D. capensis	-0.34SL + 20.10	0.005	0.51
S. salpa	0.52SL + 3.43	0.02	0.20

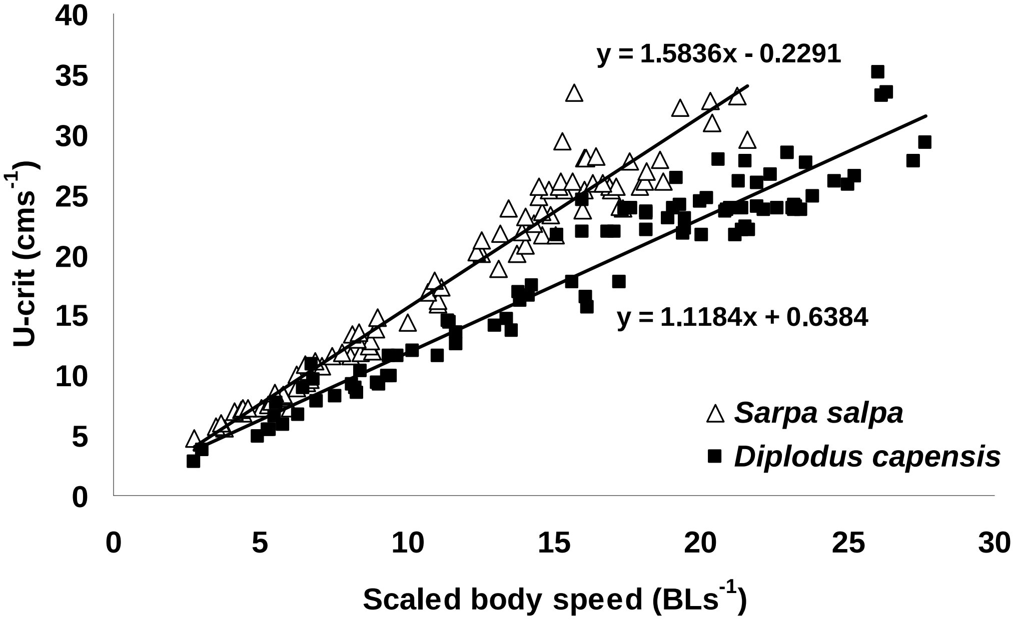

Figure 4.6: *U*-crit based on scaled body speed for warm temperate Sparidae *Diplodus capensis* and *Sarpa salpa* measured in a laboratory swimming chamber at the Port Alfred marine laboratory

Based on the *U*-crit values, 95% of the *S. salpa* individuals attained Re > 1000, and therefore were swimming in an inertial hydrodynamic environment. Only 15 % of the *D. capensis* individuals had not attained Re > 1000 and these larvae swam in an intermediate hydrodynamic environment.

More than 75 % of the swimming abilities, including both *U*-crit and endurance swimming, of *D. capensis* and *S. salpa* could by explained by the first eigenvector (Factor 1) with Principal Component Analysis (Table 4.7). For both U-crit and endurance swimming factor 1 was equally characterized by all four variables including standard length, preanal length, body depth, head length which are all indicative of growth. The second eigenvector (Factor 2) only explained 19.6 % of the swimming ability in both species for *U*-crit swimming and 18.4 % of the swimming ability in both species for endurance swimming. These two factorial axes cumulatively explained 96.0 % of the *U*-crit swimming ability and 98.1 % of the endurance swimming ability in both species (Fig. 4.7).

Table 4.7: Eigenvectors determined from PCA for morphological variables and swimming abilities of larvae

	***U*-crit**	
	Factor 1	**Factor 2**
% Variance explained	76.40	19.60
Standard length	-0.50	-0.05
Preanal length	-0.51	-0.03
Body depth	-0.49	-0.04
Head length	-0.50	-0.05
Speed	-0.09	0.99
	Endurance	
	Factor 1	**Factor 2**
% Variance explained	79.70	18.40
Standard length	-0.50	-0.06
Preanal length	-0.50	-0.07
Body depth	-0.49	-0.12
Head length	-0.49	-0.07
Distance	-0.49	0.99

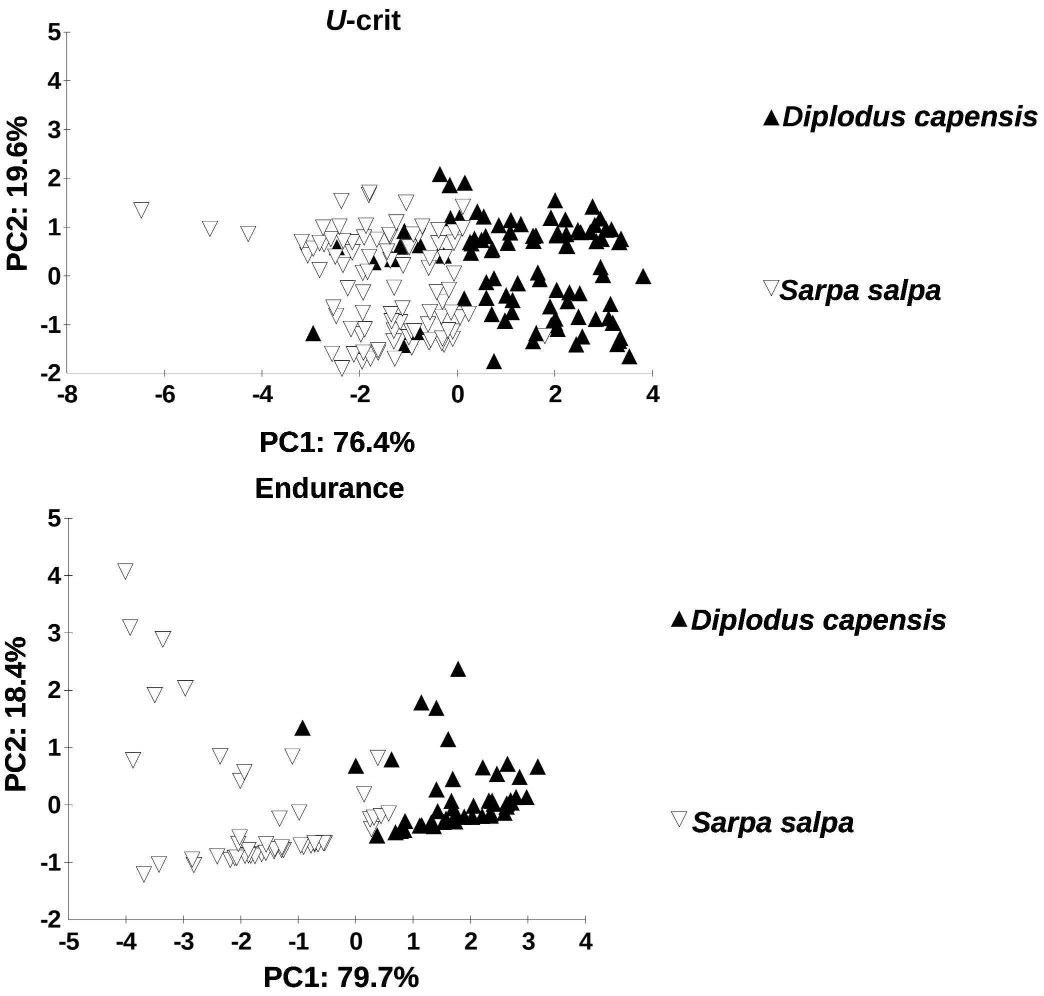

Figure 4.7: Representation of variation in swimming abilities of *Diplodus capensis* and *Sarpa salpa* in the first two axes of the PCA measured in a laboratory swimming chamber at the Port Alfred marine laboratory. Variables including standard length, preanal length, body depth, head length and swimming ability used in PCA analysis (n = 187 for U-crit; n = 96 for endurance)

5. DISCUSSION

The maximum *U*-crit (35 cms^{-1}) obtained by *D. capensis* and a maximum endurance (65 km) obtained by *S. salpa* during this study (Table 4.8), are greater than the maximum swimming abilities observed in other temperate sparid larvae studied thus far (Fukuhara, 1985; Fukuhara, 1987; Trnski, 2002; Clarke et al., 2005; Leis et al., 2006). The swimming speeds of settlement-size sparid larvae from Japan, *Pagrus major* and *Acanthopagrus schlegeli*, are slow and only reach speeds of ~4 cms^{-1} (Fukuhara, 1985; Fukuhara, 1987). These slower speeds could be a result of the methodology used by Fukuhara (1985) and Fukuhara (1987) where larvae were kept in a 700 liter circular tank and swimming speeds were recorded by observers from the outside. Sparid larvae from temperate Australia can swim at speeds up to 27 cms^{-1} and distances up to 10 km (Clarke et al., 2005) and therefore have similar swimming abilities to those recorded in the present study. However, the sizes of larvae in the present study (8.9 – 21.3 mm) are larger than those used by Clarke et al. (2005) (2.2 – 10.7 mm) which could account for the difference in the maximum *U*-crit speed (35 cms^{-1}) and maximum endurance value (65km) obtained in the present study. Furthermore, the wild-caught larvae used in the present study could have greater swimming abilities than the laboratory reared larvae obtained from aquaculture facilities in the study by Clarke et al. (2005). In the temperate study by Clarke et al. (2005) the sparid, *Acanthopagrus australis*, at a standard length of 9 – 10 mm had a mean *U*-crit speed of 21 cms^{-1} and *Pagrus auratus* at the same length had a mean of 12 cms^{-1}. In the present study *D. capensis* had a slower mean *U*-crit speed of 7.7 cms^{-1} than *A. australis* and *P. auratus*. Similarly at a length of 10 – 11 mm, *D. capensis* had a slower mean *U*-crit speed of 17.7 cms^{-1} than the temperate Australian sparid, *A. australis*, which had a mean *U*-crit of 22 cms^{-1}. For the endurance tests however *P. auratus* in the Australian studies and wild-caught *D. capensis* in the present study had the same mean endurance swimming ability (8 km) at the size interval of 8 – 9 mm. *In situ* studies of temperate Sparidae larvae in Australia have shown that these larvae have swimming speeds greater than that of ambient currents (Trnski, 2002; Leis et al., 2006). The results from Sparidae larvae in temperate regions (Trnski, 2002; Clarke et al., 2005; Leis et al., 2006) and from Sparidae larvae in the present study all suggest that these larvae have swimming abilities that allow them to actively influence their dispersal trajectories after notochord flexion.

No significant difference in *U*-crit or endurance swimming was observed between the two species. This lack in significant difference in swimming abilities between species is not surprising. Similar results were recorded by Clarke et al. (2005). Species within the same family display a similar morphology and size at settlement (Leis, 1991). Sparidae occur in both temperate and tropical oceans and larvae show very little differentiation in morphology and development at settlement (Neira et al., 1998). As these are important influences on the swimming performance of larvae, related species within a family will achieve similar swimming speeds. Late-stage larvae of both species in this study occupy the same habitat (Strydom, in press), therefore the similarity in swimming abilities could also be a result of environmental pressures that affect both species equally (Stobutzki and Bellwood, 1994). The mean standard length of *S. salpa* in both swimming experiments (*U*-crit and endurance) was larger than that of *D. capensis* since larvae of *S. salpa* usually recruit to shallow water nursery habitats at a larger size (Strydom, in press).

Table 4.8: Comparison of swimming speed and distance travelled in larvae of Sparidae from temperate oceans

Study	**Species**	**Size range (mm)**	***U*-crit (cms^{-1})**	**Endurance (km)**	***In situ* speed**
Trnski (2002)	*Acanthopagrus australis*	9.6 – 11.1			4 - 13
Clarke et al. (2005)	*Acanthopagrus australis*	4.9 – 10.7	2 – 26		
Leis et al. (2006)	*Acanthopagrus australis*	7.2 – 11.5			3 – 11.9
Fukuhara (1987)	*Acanthopagrus schlegeli*	5.0 – 11.0			1 – 3
Present study	*Diplodus capensis*	8.9 – 16.0	2.8 – 35.2	0.2 – 32.4	
Trnski (2002)	*Pagrus auratus*	10.2 – 15.0			3 - 13.5
Clarke et al. (2005)	*Pagrus auratus*	2.2 – 10.0	1 – 27	4 – 9.9	
Leis et al. (2006)	*Pagrus auratus*	7.0 – 11.5			1 – 12.4
Fukuhara (1985)	*Pagrus major*	5.0 – 7.5			1 – 4
Trnski (2002)	*Rhabdosargus sarba*	9.3 – 11.4			3.5 - 11
Present study	*Sarpa salpa*	12.1 – 21.3	4.8 – 33.4	0.07 – 64.8	

Larvae in the present study were swum without food or rest and were subjected to some degree of stress during handling. The feeding of larvae in swimming endurance experiments has shown an enhancement in the stamina of the larvae (Leis and Clarke, 2005). Even with the pressures of no food or rest in the present study, the swimming abilities attained by the larvae are comparable to those observed in temperate Australian perciform larvae (Clarke et al., 2005). It is therefore also probable that these observations are underestimates of actual swimming performances of these sparid larvae in the wild. Furthermore, it may be appropriate to use the results from best performing larvae as indicators, as high mortality rates of fish larvae occur in the wild (Houde, 1989) and only a few of the fittest larvae will survive to settlement. The best performers across both species in this study swam approximately 4 – 10 cms^{-1}

faster and 1 – 36 km further than the average larva. Best performers will therefore have a greater influence on their dispersal than the performance of the average larva.

Both species displayed an increase in swimming ability with length. Similar results were an increase in critical speed with increasing standard length have been observed in other studies (Fisher et al., 2000; Clarke et al., 2005). Standard length explained the significant variation in endurance and *U*-crit swimming abilities in *S. salpa* but was unable to explain the variation in *D. capensis*. Similar results with a lack of significant relationship between length and swimming abilities of larvae has been recorded in tropical studies on coral reef larvae in the pomacentrid and apogonid families (Fisher and Wilson, 2004). A weak positive correlation occurred between distance swum and standard length with similar results observed in Australia (Stobutzki, 1998). This is not surprising as these unfed larvae will need to rely on their stored food reserves for endurance activity. Larger larvae will therefore be able to sustain themselves for longer periods of time until exhaustion (Leis and Clarke, 2005). *Sarpa salpa* showed an increase in scaled critical speed (BLs^{-1}) with growth. Similar results were observed in sparid larvae in temperate Australia (Clarke et al., 2005). Scaled critical speed explained the significant variation in *U*-crit swimming speed which conforms to the results by Clarke et al. (2005). Temperate sparid larvae in the study by Clarke et al. (2005) had a maximum speed of 20 BLs^{-1}, and showed the greatest rate of increase (2.5 to 2.8 BLs^{-1} per mm) in scaled critical speed with growth, compared to the Sciaenidae (0.8 BLs^{-1} per mm) and Percichthyidae (-0.7 BLs^{-1} per mm) larvae in that same study. In the present study *D. capensis* increased at about 1.1 BLs^{-1} per mm while *S. salpa* increased at about 1.5 BLs^{-1} per mm.

The modal current velocity in the near surface (depth of 4 m) of the nearshore water column in the Greater Addo Marine Reserve is 8 cms^{-1} and at the bottom of the water column at a depth of 14 m was 6 cms^{-1} (Chapter 2). Most of the *D. capensis* and *S. salpa* larvae could swim faster than these modal current velocities. In addition to out-swimming currents, larvae can use vertical migration to select favourable, slower velocity currents within the water column to maintain their position (Melville-Smith et al., 1981; Leis and Carson-Ewart, 2000). Larvae are known to actively select less turbulent habitats in the surf zone in warm temperate South Africa (Watt-Pringle and Strydom, 2003). Most postflexion and settlement stage larvae can therefore actively influence their dispersal using these behavioural mechanisms and deviate from passive transport trajectories after notochord flexion.

6. CONCLUSION

This is the first study to address the swimming abilities of larvae in temperate waters of South Africa. Results from this study confirm that larvae of local Sparidae are strong swimmers, and have similar or greater swimming abilities than the sparid larvae tested thus far in temperate Australia (Trnski, 2002; Clarke et al., 2005; Leis et al., 2006). The results from the present study also highlights that these late-stage sparid larvae have swimming abilities that exceed that of local current velocities. Knowing the swimming abilities of larval fishes is fundamental to understanding dispersal patterns and recruitment processes. Models of larval fish dispersal therefore need to take all aspects of larval fish behaviour and local oceanography into account for appropriate management of fish populations and the design of marine protected areas (MPAs) (Stobutzki, 2001; Palumbi, 2003; Leis, 2003; Sale, 2004).

7. ACKNOWLEDGEMENTS

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8. REFERENCES CITED

ARMSWORTH, P.R. 2000. Modeling the swimming response of late stage larval reef fish to different stimuli. *Marine Ecology Progress Series* **195**: 231-247.

ARMSWORTH, P.R., MAURICE, K.J., BODE, L. 2001. Dispersal strategies for reef fish larvae. *American Naturalist* **157**: 434-450.

BELLWOOD, D.R., FISHER, R. 2001. Relative swimming speeds in reef fish larvae. *Marine Ecology Progress Series* **211**: 299-303.

BLAXTER, J.H.S. 1986. Development of sense organs and behavior of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society* **115**: 89-114.

BRETT, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Journal Fisheries Research Board of Canada* **21**: 1183-1226.

CLARKE, D.L., LEIS, J.M., HAY, A.C., TRNSKI, T. 2005. Swimming ontogeny of larvae of four temperate marine fishes. *Marine Ecology Progress Series* **292**: 287-300.

COETZEE, P.S. 1986. Diet composition and breeding cycle of blacktail, *Diplodus sargus capensis* (Pisces: Sparidae), caught off St Croix Island, Algoa Bay, South Africa. *South African Journal of Zoology* **21**: 237-243.

DUDLEY, B., TOLIMIERI, N., MONTGOMERY, J.C. 2000. Swimming ability of the larvae of some reef fishes from New Zealand waters. *Marine and Freshwater Research* **51**: 783-787.

FISHER, R. 2004. Nocturnal vertical distribution of late-stage larval coral reef fishes off the leeward side of Lizard Island, Great Barrier Reef, Australia. *Bulletin of Marine Science* **75**: 439-451.

FISHER, R. 2005. Swimming speeds of larval coral reef fishes: implications on self-recruitment and dispersal. *Marine Ecology Progress Series* **285**: 223-232.

FISHER, R., BELLWOOD, D.R. 2001. Effects of feeding on the sustained swimming abilities of late-stage larval *Amphiprion melanopus*. *Coral Reefs* **20**: 151-154.

FISHER, R., BELLWOOD, D.R. 2002. The influence of swimming speed on sustained swimming performance of late-stage reef fish larvae. *Marine Biology* **140**: 801-807.

FISHER, R., BELLWOOD, D.R. 2003. Undisturbed swimming behaviour and nocturnal activity of coral reef fish larvae. *Marine Ecology Progress Series* **263**: 177-188.

FISHER, R., WILSON, S.K. 2004. Maximum sustainable swimming speeds of late-stage larvae of nine species of reef fishes. *Journal of Experimental Marine Biology and Ecology* **312**: 171-186.

FISHER, R., BELLWOOD, D.R., JOB, S.D. 2000. Development of swimming abilities in reef fish larvae. *Marine Ecology Progress Series* **202**: 163-173.

FISHER, R., LEIS, J.M., CLARKE, D.L., WILSON, S.K. 2005. Critical swimming speeds of late-stage coral reef fish larvae: variations within species, among species and between locations. *Marine Biology* **147**: 1201-1212.

FRANK, K.T., CARSCADDEN, J.E., LEGGETT, W.C. 1993. Causes of spatio-temporal variation in the patchiness of larval fish distributions: differential mortality or behaviour? *Fisheries Oceanography* **2**: 114-123.

FUKUHARA, O. 1985. Functional morphology and behavior of early life stages of Red Sea Bream. *Bulletin of the Japanese Society of Scientific Fisheries* **51**: 731-743.

FUKUHARA, O. 1987. Larval development and behaviour in early life stages of Black Sea Bream reared in the laboratory. *Nippon Suisan Gakkaishi* **53**: 371-379.

HEEMSTRA, P.C., HEEMSTRA, E. 2004. Coastal fishes of Southern Africa. South African Institute for Aquatic Biodiversity and National Inquiry Service Centre, Grahamstown 488 pp.

HOUDE, E.D. 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). *Journal of the Fisheries Research Board of Canada* **26**: 1647-1659.

HOUDE, E.D. 1989. Subtleties and episodes in the early life of fishes. *Journal of Fish Biology* **55**: 215-226.

JENKINS, G.P., WELSFORD, D.C. 2002. The swimming abilities of recently settled post-larvae of *Sillaginodes punctata*. *Journal of Fish Biology* **60**: 1043-1050.

LAURENCE, G.C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (*Micropterus salmoides*). *Journal of Fish Biology* **4**: 73-78.

LEIS, J.M. 1991. The pelagic stage of reef fishes: The larval biology of coral reef fishes. Academic Press, New York 183-230.

LEIS, J.M. 2003. What does the larval fish biology tell us about the design and efficacy of marine protected areas. Aquatic protected areas: What works best and how do we know? Australian Society for Fish Biology, North Beach, WA pp. 170-180,

LEIS, J.M. 2006. Are larvae of demersal fishes plankon or nekton? *Advances in Marine Biology* **51**: 59-141.

LEIS, J.M., CARSON-EWART, B.M. 1997a. In situ swimming speeds of the late pelagic larvae of some Indo-Pacific coral-reef fishes. *Marine Ecology Progress Series* **159**: 165-174.

LEIS, J.M., CARSON-EWART, B.M. 1997b. Swimming speeds of the late larvae of some coral reef fishes. *Marine Ecology Progress Series* **159**: 165-174.

LEIS, J.M., CARSON-EWART, B.M. 1998. Complex behaviour by coral-reef fish larvae in open water and near-reef pelagic environments. *Environmental Biology of Fishes* **53**: 259-266.

LEIS, J.M., CARSON-EWART, B.M. 1999. *In situ* swimming and settlement behaviour of larvae of an Indo-Pacific coral-reef fish, the Coral Trout (Pisces, Serranidae, *Plectropomus leopardus*). *Marine Biology* **134**: 51-64.

LEIS, J.M., CARSON-EWART, B.M. 2000. Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. *Coral Reefs* **19**: 247-257.

LEIS, J.M., CLARKE, D.L. 2005. Feeding greatly enhances endurance swimming of settlement-stage reef-fish larvae (Pomacentridae). *Ichthyological Research* **52**: 185-188.

LEIS, J.M., STOBUTZKI, I.C. 1999. Swimming performance of late pelagic larvae of coral reef fishes: *in situ* and laboratory-based measurements. Proceedings of the 5th Indo-Pacific Fish Conference Noumea 575-583.

LEIS, J.M., HAY, A.C., TRNSKI, T. 2006. In situ ontogeny of behaviour in pelagic larvae of three temperate marine, demersal fishes. *Marine Biology* **148**: 655-669.

LEIS, J.M., SWEATMAN, H.P.A., READER, S.E. 1996. What the pelagic stages of coral reef fishes are doing out in the blue water: daytime field observations of larval behaviour. *Marine and Freshwater Research* **47**: 401-411.

MELVILLE-SMITH, R., BAIRD, D., WOOLDRIDGE, T.H. 1981. The utilization of tidal currents by the larvae of an estuarine fish. *South African Journal of Zoology* **16**: 10-13.

MILLER, T.J., CROWDER, L.B., RICE, J.A., MARSCHALL, E.A. 1988. Larval size and recruitment mechanisms in fishes: towards a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1657-1670.

MONTGOMERY, J.C., TOLIMIERI, N., HAINE, O. 2001. Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries* **2**: 261-277.

MOSER, H.G., RICHARDS, W.J., COHEN, D.M., FAHAY, M.P., KENDALL, A.W., RICHARDSON, S.L. 1984. Ontogeny and systematics of fishes. *American Society of Ichthyologists and Herpetologists Special Publication* **1**: 1-760.

NEIRA, F.J., MISKIEWICZ, A.G., TRNSKI, T. 1998. Larvae of Temperate Australian fishes. Laboratory guide for larval fish identification. University of Western Australia Press, Nedlands 474 pp.

PALUMBI, S.R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* **13**: S146-S158.

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

ROBERTS, C.M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**: 1454-1456.

SALE, P.F. 2004. Connectivity, recruitment variation, and the structure of reef fish communities. *Integrative and Comparative Biology* **44**: 390-399.

SMALE, M.J., BUXTON, C.D. 1989. The subtidal gully fish community of the Eastern Cape and the role of this habitat as a nursery area. *South African Journal of Zoology* **24**: 58-67.

SMITH, M.M., HEEMSTRA, P.C. 1995. Smith's Sea Fishes. Macmillan, Johannesburg, South Africa. 1047pp.

STOBUTZKI, I.C. 1998. Interspecific variation in sustained swimming ability of late pelagic stage reef fish from two families (Pomacentridae and Chaetodontidae). *Coral Reefs* **17**: 111-119.

STOBUTZKI, I.C. 2001. Marine reserves and the complexity of larval dispersal. *Reviews in Fish Biology and Fisheries* **10**: 515-518.

STOBUTZKI, I.C., BELLWOOD, D.R. 1994. An analysis of the sustained swimming abilities of pre- and post-settlement coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **175**: 275-286.

STOBUTZKI, I.C., BELLWOOD, D.R. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Marine Ecology Progress Series* **149**: 35-41.

STRYDOM, N.A. 2003. Occurrence of larval and early juvenile fishes in the surf zone adjacent to two intermittently open estuaries, South Africa. *Environmental Biology of Fishes* **66**: 349-359.

STRYDOM, N.A. In press. Small subtidal bays: a new larval fish nursery identified along temperate rocky shores, South Africa. *African Zoology*.

TRNSKI, T. 2002. Behaviour of settlement-stage larvae of fishes with an estuarine juvenile phase: in situ observations in a warm-temperate estuary. *Marine Ecology Progress Series* **242**: 205-214.

WARDLE, C.S. 1975. Limit of fish swimming speed. *Nature* **255**: 725-727.

WATT-PRINGLE, P., STRYDOM, N.A. 2003. Habitat use by larval fishes in a temperate South African surf zone. *Estuarine, Coastal and Shelf Science* **58**: 765-774.

WEBB, P.W., WEIHS, D. 1986. Functional locomotor morphology of early life history stages of fishes. *Transactions of the American Fisheries Society* **115**: 115-127.

WESTERNHAGEN, H.V., ROSENTHAL, H. 1979. Laboratory and in-situ studies on larval development and swimming performance of Pacific herring *Clupea harengus pallasi*. *Helgoländer Wissenschaftliche Meeresuntersuchungen* **32**: 539-549.

WHITFIELD, A.K. 1998. Biology and ecology of fishes in South African Estuaries. Ichthyological Monographs of the JLB Smith Institute for Ichthyology, No. **2**: Grahamstown 232 pp.

WIESER, W., KAUFMANN, R. 1998. A note on interactions between temperature, viscosity, body size and swimming energetics in fish larvae. *Journal of Experimental Biology* **201**: 1369-1372.

CHAPTER 5

SYNTHESIS AND CONCLUSIONS

In South Africa, coastal habitats including estuaries and surf zones are known to function as nursery areas for both the larval and juvenile stages of many marine fish species (Lasiak, 1986; Whitfield, 1998; Strydom et al., 2003). These fish species will spawn in or near these coastal habitats to provide the early life stages with a favourable habitat for development (Potter et al., 1990; Chute and Turner, 2001; Strydom et al., 2003). In South Africa however, the use of the shallow nearshore habitat by larval fishes and the link between larval fish assemblages in the shallow nearshore and the adjacent coastal habitats is poorly understood. An understanding of local current velocities and directions which occur within the shallow nearshore will allow for a better understanding of dispersal dynamics of larvae (Leis, 2006). Ocean currents are known to play an important role in determining the distribution of larval fishes (Leis and Goldman, 1983), yet South African research on shallow water currents characterizing the shallow nearshore is lacking. The elucidation of nearshore dynamics in relation to larval fish occurrence must take larval behaviour, particularly swimming abilities, into consideration. However, the horizontal swimming abilities of larval fish, which are known to have a profound influence on the dispersal or retention of larvae within coastal habitats (Stobutzki and Bellwood, 1997), is unknown in South Africa. Models of dispersal are imperative in determining the geographical extent of marine fish populations which has implications on the management of fisheries and the design of marine protected areas (MPAs) (Miller et al., 1988; Cowen et al., 2000; Leis, 2002). The present study assessed the composition, seasonality, abundance and distribution of larval fishes in the shallow nearshore of a proposed MPA in the eastern sector of Algoa Bay. The dynamics of larval fishes were related to the current flow patterns characterizing the study area. In addition, larval swimming abilities were assessed to further expand discussion on the transport of eggs and larvae to and from the proposed MPA.

In the shallow nearshore of eastern Algoa Bay, a high species diversity was recorded with 78 species represented in the sampling area in the eastern half of Algoa Bay.

This is greater than the number of species (36 species) observed in the western sector of the Bay (Beckley, 1986). The gobiids dominated catches, particularly off the Sundays Estuary mouth but other fish families including the Engraulidae, Clupeidae, Sparidae and Cynoglossidae made important contributions to the overall larval fish catch. Dominant species in the bay included *Engraulis capensis*, *Sardinops sagax*, *Caffrogobius nudiceps* and an unidentified goby 4. Larvae of marine fish species dominated the catch but a completely different pattern occurs in the larval fish assemblage typically occurring in the adjacent surf zone. Surf zones are dominated (>90 %) by larvae of estuary associated marine species (Whitfield, 1989; Strydom and d'Hotman, 2005). Larvae of coastal species that produce benthic eggs dominated the shallow nearshore catch. Similar results were obtained in the western sector of Algoa Bay (Beckley, 1986). Larval fish density displayed seasonality, peaking in spring with a mean density of 64 larvae/100m^3, ranging to a maximum of >700 larvae/100m^3. Density of larvae in the shallow nearshore was greatest along the deeper ~15 m contour (40 larvae/100m^3) than the ~5 m depth contour (30 larvae/100m^3). Larvae at the preflexion stage of development dominated catches in this study although all developmental stages were observed. This shows a high degree of local hatching occurring in the area. Another pattern that emerged was that larvae of estuary associated marine species generally had longer standard lengths close to shore, along the ~5 m depth contour when compared with catches of the same species along the ~15 m depth contour. Similar findings were made in the warm temperate waters of the Eastern Cape (Strydom, 2007)and in subtropical KwaZulu Natal (Harris et al., 2001). This data supports the shoreward movement hypothesis where the larvae of estuary associated marine fishes will move passively initially and then later by active swimming from offshore spawning grounds to surf zones (Boehlert and Mundy, 1988).

Two dominant current flow patterns were observed in the study area from data collected using a bottom-moored ADCP over a period of one year (May 2006 – May 2007). An offshore flowing south eastward current, which near the surface of the water column (4 m), flowed 36 % of the time and at the bottom of the water column (14 m), flowed 40 % of the time. The second dominant current, an inshore north westward current, flowed near the surface and at the bottom of the water column, 32 % of the time. The south westward current near the surface of the water column flowed 18 % of the time and at the bottom of the water column only flowed 15 % of the time. The presence of the north eastward current was similarly less frequent and near the surface only flowed 14 % and at the bottom only flowed 13 % of the time. Velocities within the study area ranged from 0 to >100 cms^{-1}. However, a modal velocity of 8 cms^{-1} near the surface (4 m) and 6 cms^{-1} at the bottom (14 m) of the water column was recorded during this study. Current velocities within the nearshore were typically greatest near the surface of the water column (4 m) with a mean velocity of ~30 cms^{-1}, but decreased exponentially to a mean of ~10 cms^{-1} at a depth of 14 m.

Eggs and preflexion larvae are, to a certain extent, passive particles in the water column and dispersal will be influenced by local wind and tide driven current flow patterns (Roberts, 1997). Using current velocity and direction data generated from the present study an indication of the potential transport of passive eggs and preflexion larvae spawned within the proposed MPA can be generated. Larvae of coastal species that produce benthic eggs dominate catches within Algoa Bay, therefore bottom currents are effective in dispersing these benthic eggs. During the main spawning season in spring and summer, eggs and preflexion larvae have the potential to be transported, at the bottom of the water column, 186 km east from the moored ADCP in the centre of the study area, placing propagules near Kidds Beach (33°05'31"S, 27°48'26"E), south of the city of East London. This information may serve as a guideline in the placement of neighbouring marine protected areas. During winter and autumn however, bottom dispersal is minimal leading to entrainment of bottom eggs in the bay.

Larval dispersal is however far more complicated than simple passive transport (Leis, 2003) and this proposed dispersal distance is probably an over estimation. Larval fishes are known to be capable swimmers with keen sensory abilities enabling them to select and maintain their position in preferred habitats (Kingsford et al., 2002; Leis and Carson-Ewart, 2003). To understand the dispersal of fish larvae in the marine environment, it is essential to understand local oceanography as well as larval fish behaviour, particularly the development of swimming abilities in larvae. The late stage larval swimming abilities of two common inshore sparid species which have an important recreational linefish status, *Diplodus capensis* and *Sarpa salpa*, (Smith and

Heemstra, 1995), were tested. Larvae of *D. capensis* and *S. salpa* are found abundantly in small rocky bays along the temperate coastline of South Africa (Strydom, in press). The swimming abilities of most late stage larvae of *D. capensis* and *S. salpa* exceed the modal (6 cms^{-1} at the bottom and 8 cms^{-1} near the surface of the water column) and average current velocities (18 cms^{-1}) observed in the shallow nearshore of the proposed marine protected area in Algoa Bay. The mean *U*-crit value for *D. capensis* (18.6 cms^{-1}) was similar to that of *S. salpa* (18.0 cms^{-1}), whereas mean endurance (km swum) was greater in *S. salpa* (8.4 km) than *D. capensis* (5.9 km). These results indicate that these larvae have swimming abilities greater than shallow nearshore currents observed in the proposed MPA where they occur, proving that these larvae can influence their distribution in the shallow nearshore.

Passive transport via ocean currents is only one component in understanding or modeling dispersal of fish larvae. The actual behaviour of larvae is complex, even at the preflexion stage. During the early stages of development, larvae have the ability to adjust their vertical distribution within the water column by inflating or deflating their gas bladder, to select for favourable currents (Melville-Smith et al., 1981; Leis and Carson-Ewart, 2000) even with poor swimming abilities. After flexion with the onset of caudal fin development, larvae begin to have stronger swimming abilities and develop sensory abilities that allow for active habitat selection (Leis, 2003; Leis, 2006).

Furthermore, larvae of coastal species that produce benthic eggs dominate catches within Algoa Bay. These larvae are larger and have better developed sensory and swimming abilities than larvae from pelagic eggs. They will therefore develop quicker than larvae from pelagic eggs and will not be transported as far offshore (Leis, 1993; Leis, 1994). A high degree of self-recruitment is known to occur in coral reef fish populations, with larvae remaining close to the area where they were spawned with limited dispersal (Swearer et al., 1999; Jones et al., 1999). In spite of current patterns which could aid in the wide dispersal of larval fishes, a tagging study on larval damselfishes has shown that the larvae are retained close to their natal reef (Jones et al., 1999). This self-recruitment is also highly probable in warm temperate waters where some adult fish species are highly resident (Brouwer et al., 2003). This evidence suggests that dispersal in larvae and therefore connectivity in marine populations is difficult to predict.

In conclusion results from this study indicate that the proposed MPA is situated in a functioning spawning area for many coastal fish species. The shallow nearshore of Algoa Bay can also be regarded as a nursery area with all developmental stages of some important recreational and commercial species occurring in the area. Current flow and direction is highly dynamic within the shallow nearshore yet patterns of flow are predictable and driven by seasonal winds. Other unknown drivers will also account for the variability in flow patterns and could include the coastal landscape and the presence of Bird Island at the eastern extent of the bay. Currents are important in aiding or impeding larval fish transport (Leis and Goldman, 1983). The present study has also shown that late-stage sparid larvae are effective swimmers with speeds that exceed that of local current velocities in Algoa Bay. Larval dispersal will therefore deviate from that predicted by current flow alone. Furthermore orientation cues, which could include sound and salinity anomalies, are unknown in sparids and have important implications on dispersal. Larval dispersal is complex and is often poorly understood, which in the past has resulted in an overestimation of passive larval dispersal via ocean currents (Williams et al., 1984; Roberts, 1997). Assessments of dispersal should incorporate both oceanographic conditions and larval fish biology in order to understand larval fish dynamics.

REFERENCES CITED

BECKLEY, L.E. 1986. The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. *South African Journal of Zoology* **21**: 244-252.

BOEHLERT, G.W., MUNDY, B.C. 1988. Roles of behaviour and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* **3**: 51-67.

BROUWER, S.L., GRIFFITHS, M.H., ROBERTS, M.J. 2003. Adult movement and larval dispersal of *Argyrozona argyrozona* (Pisces: Sparidae) from a temperate marine protected area. *African Journal of Marine Science* **25**: 395-402.

CHUTE, A.S., TURNER, J.T. 2001. Plankton studies in Buzzards Bay, Massachusetts, USA.V. Ichthyoplankton, 1987 to 1993. *Marine Ecology Progress Series* **224**: 45-54.

COWEN, R.K., LWIZA, K.M.M., SPONAUGLE, S., PARIS, C.B., OLSON, D.B. 2000. Connectivity of marine populations: open or closed? *Science* **287**: 857-859.

HARRIS, S.A., CYRUS, D.P., BECKLEY, L.E. 2001. Horizontal trends in larval fish diversity and abundance along an ocean-estuarine gradient on the Northern KwaZulu-Natal Coast, South Africa. *Estuarine, Coastal and Shelf Science* **53**: 221-235.

JONES, G.P., MILICICH, M.J., EMSLIE, M.J., LUNOW, C. 1999. Self-recruitment in a coral reef fish population. *Nature* **402**: 802-804.

KINGSFORD, M.J., LEIS, J.M., SHANKS, A., LINDEMAN, K., MORGAN, S., PINEDA, J. 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* **70**: 309-340.

LASIAK, T.A. 1986. Juveniles, food and the surf zone habitat: implications for teleost nursery areas. *South African Journal of Zoology* **21**: 51-56.

LEIS, J.M. 1993. Larval fish assemblages near Indo-Pacific coral reefs. *Bulletin of Marine Science* **53**: 362-392.

LEIS, J.M. 1994. Coral sea atoll lagoons: closed nurseries for the larvae of a few coral reef fishes. *Bulletin of Marine Science* **54**: 206-227.

LEIS, J.M. 2002. Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. *Environmental Biology of Fishes* **65**: 199-208.

LEIS, J.M. 2003. What does the larval fish biology tell us about the design and efficacy of marine protected areas. Aquatic protected areas: What works best and how do we know? Australian Society for Fish Biology, North Beach, WA pp. 170-180,

LEIS, J.M. 2006. Are larvae of demersal fishes plankon or nekton? *Advances in Marine Biology* **51**: 59-141.

LEIS, J.M., CARSON-EWART, B.M. 2000. Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. *Coral Reefs* **19**: 247-257.

LEIS, J.M., CARSON-EWART, B.M. 2003. Orientation of pelagic larvae of coral-reef fishes in the ocean. *Marine Ecology Progress Series* **252**: 239-253.

LEIS, J.M., GOLDMAN, B. 1983. Studies on the biology of larval fishes in the Lizard Island area, Northern Great Barrier Reef. Proceedings: Inaugural Great Barrier Reef Conference James Cooke University Press, Townsville 221-225.

MELVILLE-SMITH, R., BAIRD, D., WOOLDRIDGE, T.H. 1981. The utilization of tidal currents by the larvae of an estuarine fish. *South African Journal of Zoology* **16**: 10-13.

MILLER, T.J., CROWDER, L.B., RICE, J.A., MARSCHALL, E.A. 1988. Larval size and recruitment mechanisms in fishes: towards a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1657-1670.

POTTER, I.C., BECKLEY, L.E., WHITFIELD, A.K., LENANTON, R.C.J. 1990. Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and Southern Africa. *Environmental Biology of Fishes* **28**: 143-178.

ROBERTS, C.M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**: 1454-1456.

SMITH, M.M., HEEMSTRA, P.C. 1995. Smith's Sea Fishes. Macmillan, Johannesburg, South Africa. 1047 pp.

STOBUTZKI, I.C., BELLWOOD, D.R. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Marine Ecology Progress Series* **149**: 35-41.

STRYDOM, N.A. 2007. Jetski-based plankton towing as a new method of sampling larval fishes in shallow marine habitats. *Environmental Biology of Fishes* **78**: 299-306.

STRYDOM, N.A. In press. Small subtidal bays: a new larval fish nursery identified along temperate rocky shores, South Africa. *African Zoology*.

STRYDOM, N.A., D'HOTMAN, B.D. 2005. Estuary-dependence of larval fishes in a non-estuary associated South African surf zone: evidence for continuity of surf assemblages. *Estuarine, Coastal and Shelf Science* **63**: 101-108.

STRYDOM, N.A., WHITFIELD, A.K., WOOLDRIDGE, T.H. 2003. The role of estuarine type in characterizing early stage fish assemblages in warm temperature estuaries, South Africa. *African Zoology* **38**: 29-43.

SWEARER, S.E., CASELLE, J.E., LEA, D.W., WARNER, R.R. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* **402**: 799-802.

WHITFIELD, A.K. 1989. Ichthyoplankton in a southern African surf zone: Nursery area for the postlarvae of estuarine associated fish species? *Estuarine, Coastal and Shelf Science* **29**: 533-547.

WHITFIELD, A.K. 1998. Biology and ecology of fishes in South African Estuaries. Ichthyological Monographs of the JLB Smith Institute for Ichthyology, No. **2**: Grahamstown 232 pp.

WILLIAMS, D.Mc.B., WOLANSKI, E., ANDREWS, J.C. 1984. Transport mechanisms and their potential movement of planktonic larvae in the central region of the Great Barrier Reef. *Coral Reefs* **2**: 236-239.