LARVAL FISH ASSEMBLAGES OF SELECTED ESTUARINE AND COASTAL SYSTEMS IN KWAZULU-NATAL, SOUTH AFRICA

by

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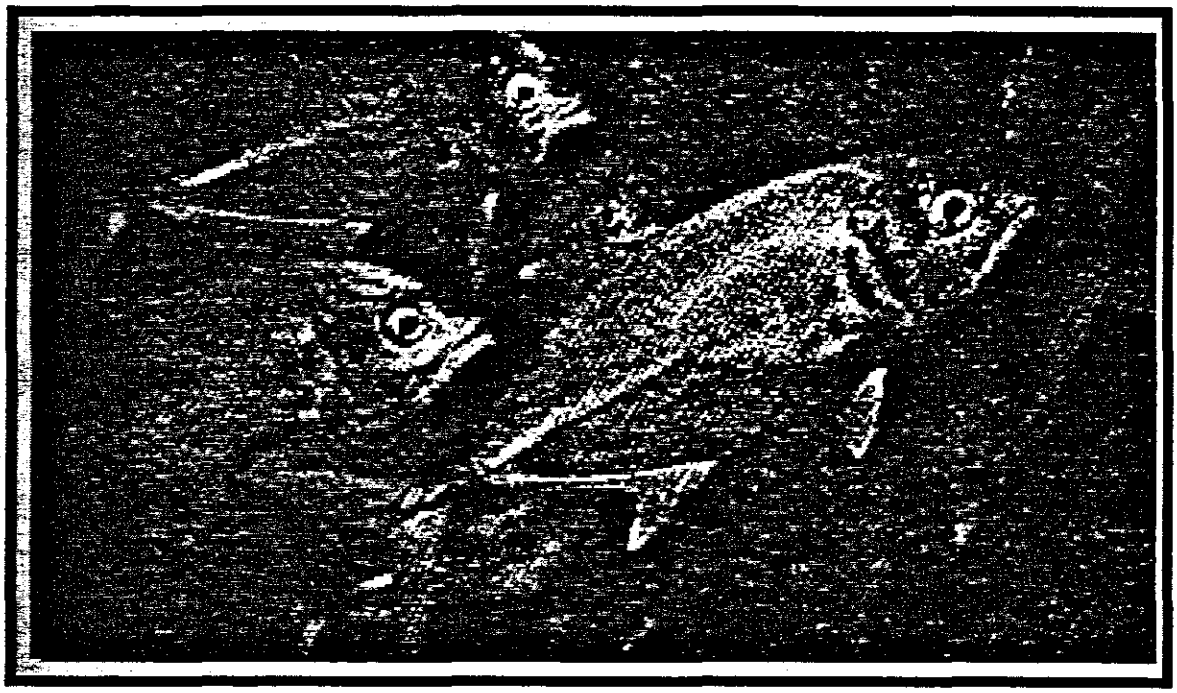
DECLARATION

I hereby declare that this whole thesis is my own original work, and to the best of my knowledge, it contains no material previously published or written by another person nor material submitted in any form for the award of any degree at another university. Where use was made of the work of others it has been duly acknowledged in the text.

Dedication

I dedicate this thesis to my parents, David and Eileen Harris, who provided me with the opportunity and the inspiration to pursue a career in Marine Biology and to attain this level of achievement.



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ABSTRACT

ABSTRACT

This study focuses describing assemblages of fish larvae occurring in potential nursery habitats and elucidating the recruitment processes of fishes in the KwaZulu-Natal region. The composition, the degree of estuarine-association of all taxa, temporal and spatial abundance patterns, developmental stages and were examined in three large estuarine systems, a surf zone habitat and in the nearshore marine environment. In addition, two 24-h inlet studies were undertaken to ascertain diel patterns. Relationships between larval densities with environmental variables were also examined to gain insight into the possible causal mechanisms for the observed abundance patterns.

Larval fish samples from Durban Harbour and Richards Bay Harbour were collected at top, mid and bottom depths in the dredged channel 100 to 200 m from the harbour entrance, over 13 and 12 month study periods, respectively. Larval fish from the St Lucia Estuary were collected over 12 months at a fixed station 4 km from the mouth. A total of 8 797 fish larvae, representing 64 families and 144 taxa, was collected in Durban Harbour. From Richards Bay Harbour, 105 taxa representing 53 families were collected from a total of 7 163 larvae. Larvae of the thorny anchovy, *Stolephorus holodon*, were very abundant in both harbours (32% and 10% of the total catch, respectively), with the blueline herring *Herklotsichthys quadrimaculatus* (30%) and an unidentified goby Gobiid 12 (9%) being dominant in Durban Harbour and in Richards Bay Harbour, respectively. Conversely, in the St Lucia Estuary, 51 590 larvae in total were collected represented by 85 taxa from 44 families. The river goby *Glossogobius callidus* (67%) and the estuarine roundherring *Gilchristella aestuaria* (19%) were the most dominant species.

Larval fish in the surf zone were collected monthly, using a pushnet, at six stations up to 3 km north of the St Lucia Estuary mouth. To determine any diel patterns a 24-h study was also undertaken in the surf zone when the estuary mouth was closed. Far more larvae were collected during the 24-h study compared to the 12-month study: 13 731 larvae and 2 931 larvae, respectively. The larval assemblage was characterised by taxa in the families Sparidae, Haemulidae, Ambassidae, Tripterygiidae and Chanidae. The most abundant species were *Pomadasys olivaceum*, *Ambassis* sp.,

Rhabdosargus holubi, *Croilia mossambica* and *Chanos chanos*. Fish larvae were also sampled in the adjacent nearshore coastal zone, from five stations in a transect up to 2.5 km offshore, and from two stations north and south of the St Lucia Estuary mouth. The assemblage consisted of 246 taxa representing 98 families from a total of 6 069 larvae. Larvae in the families Myctophidae and Tripterygiidae comprised 21% and 16% of the total catch, with the dominant species being an unidentified triplefin, Tripterygiid 1, and the lanternfish *Benthosema fibulatum*.

The percentage contribution to total number of larvae of estuarine-associated fish species increased from "estuarine-habitat" (St Lucia Estuary) to "semi-estuarine habitat" (Richards Bay Harbour and the surf zone) to "marine-habitat" (Durban Harbour and the nearshore coastal zone). Species representative of each estuarine-association group were, for example: *G.aestuaria*, *Thryssa vitrirostris* and *Rhabdosargus* spp.- estuarine-dependent; *S.holodon*, *C.mossambica* and *Ambassis* spp - partially estuarine-dependent; unidentified gobies (Gobiid 12 and Gobiid 27), unidentified triplefins (Tripterygiid 1), *Lampanyctus alatus*, *H.quadrimaculatus* and *Umbrina ronchus* - estuarine-independent. In all study areas, different recruitment periods were evident for each estuarine-association group with peaks in abundance occurring in all four seasons. This was dependent upon the seasonality of the dominant species present in a particular study area.

In the estuarine environments, young larvae (preflexion and flexion developmental stages) of estuarine-dependent species were moderately abundant whereas, old larvae (postflexion) and early juveniles of partially estuarine-dependent species predominated. The surf zone habitat was dominated by postflexion larvae (68% of total catch) of estuarine-associated species, with early juveniles of estuarine-independent species being prevalent in the 24-h study when the estuary mouth was closed (50%). In the nearshore coastal environment larvae of marine species not dependent of estuaries were mainly at the preflexion and flexion developmental stages (67% of the total catch).

Stepwise regression statistics and multivariate analysis (classification and ordination) clearly indicated the importance of environmental factors in determining the structured of the larval fish assemblages. Furthermore, the correlations of larval densities with environmental variables was found to be species-specific. The most

significant variable accounting for the observed distributional patterns of the fish larvae was turbidity (ρ_w = 0.55 - weighted Spearmans rank correlation). However, the intercorrelations between all the environmental variables measured were also important in determining abundance patterns (e.g. ρ_w = 0.48 for salinity + turbidity; ρ_w = 0.41 for salinity + temperature + turbidity).

Analyses of tidal exchange of fish larvae on flood and ebb tides, in Durban Harbour, Richards Bay Harbour and in the St Lucia Estuary mouth, indicated that selective tidal stream transport is a recruitment mechanism employed by certain species (e.g. *Argyrosomus* sp., *Pomadasys commersonnii* and *Solea bleekeri*) to enable retention in the estuarine habitat i.e. larval densities of these species were significantly higher on flood tides and in bottom waters ($P < 0.05$).

In conclusion, results of the present study have indicated that diverse and dynamic larval fish assemblages are present in the estuarine and coastal systems on the KwaZulu-Natal coast. Larvae (mainly postflexion) of estuarine-associated fish species were abundant in all three estuarine systems and the surf zone suggesting that all these habitats function as nursery sites for particular species. Additional species-specific studies on larval stages of recreational and commercially important linefish species are needed in order to make management decisions regarding the conservation and exploitation of these species.

INGQIKITHI

Lesi sifundo sibheka ukuqoqwa kwamaqanda ezinhlanzi atholakala ezindaweni avame kuzona ngenhloso yokuveza obala umgudu wohlelo olulandelwa ekuqoqekeni kwezinhlanzi esifundeni saKwaZulu-Natali. Ukwakheka kanye nokuthi lolo hlobo luthanda kangakanani ukuhlala endaweni eyisizalo somfula, ukuhlala kwesikhashana kanye nendawo oluyikhonzile, kanye nezindlela zokukhula, konke lokhu kuhlolwe ezizalweni zemifula ezintathu ezinkulu, endaweni enamadlambi ngasogwini lolwandle kanye nendawo esosebeni lolwandle. Kwaphinda futhi kwaba khona izifundo ezimbili ezithatha ubusuku nemini ngasinye. Ukuhambisana kobuningi bamaqanda kanye nendawo lapho amaqanda atholakale khona kwahlolisiswa ukuze kuqondakale okungase kube yizimbangela zokudaleka ngobuningi kwalawo maqanda okuyikhona okwakuhlolwa.

Amasampula amaqanda ezinhlanzi aqoqwa echwebeni laseThekwini kanye naseRichards Bay, ngaphezulu, maphakathi nendawo kanye nasekujuleni emiseleni eqoqwe isihlabathi, endaweni engaba amamitha ayi-100 kuya kwangama-200 kusuka echwebeni esikhathini esiyizinyanga eziyi-13 kanye neziyi-12. Amaqanda ezinhlanzi atholakala esizalweni somfula e St Lucia aqoqwa esikhathini esingaba yizinyanga eziyi-12 esiteshini esiyibanga elingu 4km kusukela esizalweni somfula. Isamba esingu 8 797 samaqanda ezinhlanzi esimele imindeni engama-64 kanye nezinhlobo eziyi-144 saqoqwa echwebeni laseThekwini.Echwebeni aseRichards Bay kwaba yimindeni eyi-105 emele imindeni engama-53 ehlaanganisa isamba samaqanda ayi-7 163. Amaqanda e-thorny anchovy, *Stolephorus holodon,* ayemaningi kuwo omabili amachweba (32% no10% wesemba sonke njengokulandelana kwawo), bese kuthi i-blueline herring *Herklotsichthys quadrimculatus* (30%) kanye nenye inhlobo engacwaningwisisiwe kahle okuthiwa yi-goby Gobiid 12 (9%) okuyiyona nhlobo eningi kakhulu eThekwini kanye naseRichards Bay. Kanti e St Lucia Estuary khona kwatholakala amaqanda angama 51 590, okwathi kuleso samba u 85 yizinhlobo ezimele imindeni egama-44. I-goby yasemfuleni *Glossogobius callidus* (67%) kanti i-round herring evame esizalweni semifula *Gilchristella aestuaria* (19%) kwaba yilona hlobo lwalululuningi kakhulu.

Amaqanda atholakala emadlambini olwandle ayeqoqwa njalo ngenyananga kusetshenziswa inetha eziteshini eziyisi-6 kuze kube sebangeni elingaba ama-3 km

eNyakatho nesizalo sase St Lucia. Kwenziwa izifundo zokuqapha ezathatha ubusuku nemini ngenkathi isizalo sisavaliwe. Ngalesi sikhathi kwatholakala amaqanda amaningi kakhulu uma kuqathaniswa nasezinyangeni eziyi-12 ezazendulele: kwatholaka amaqanda ayizi-13 731 kanye nayizi-2 931 kulezi zindawo ngokulandelana kwazo. Ekuqoqweni kwamaqanda kwakuvame kakhulu izinhlobo zemindeni ye Sparidae, Ambassidae, Tripterygiidae kanye ne-Chanidae. Uhlobo okuyilona olwalande kakhulu yi*Pomadays olivaceum*, i-*Ambassis* sp., i-*Rhabdosargus holubi*, i-*Croilia mossambica kanye ne-Chanos chanos*. Amaqanda ezinhlanzi aqoqwa ogwini lwezindawo ezakhelene nalezi, eziteshini eziyisi-5, ebangeni elingaba u-2.5 km ukusuka ogwini, kanye futhi nakwezinye iziteshi ezimbili eNyakatho kanye naseNingizimu yesizalo i-St Lucia Estuary. Ukuqoqa kwakwakhiwe yizinhlobo ezingama-246 ezazimele imindeni engama-98 ethathwe esambeni esiyizi-6 069 samaqanda. Amaqanda ohlobo lwemindeni ye-Myctophidae kanye ne-Tripterygiidae ayakhe u-21% no 16% esamba sonke esaqoqwa, okwakukuningi kuso uhlobo olungakacwaningisiswa i-triplefin (Tripterygiid 1) kanye ne-lanternfish (*Benthosema fibulatum*).

Umnikelo wonke wokuqoqwa kwezinhlobo zamaqanda ezinhlanzi otholakala esizalweni somfula ngokwamaphesenti wakhuphuka usuka endaweni eyisizalo somfula (St Lucia Estuary) kuye kuleyo ezishaya sasizalo somfula (Ichweba laseRichards Bay kanye namadlambi asolwandle) kuze kube indawo yasolwandle (Ichweba laseThekwini kanye nogu). Uhlobo olumele leso naleso sizalo, uma sesithatha isibonelo, kwaku ama-*G.aestuaria*, ama-*Thryssa vitrirostris* kanye nama-*Rhabdosargus* spp - anqike kakhulu esizalweni, ama-*S.holodon*, *C.mossambica* kanyenama-*Ambassis* spp - asakunqika kumpilo yasesizalweni somfula, ama-gobies angakacwaningisisiswa (ama-Gobiid 12 kanye nama-Gobiid 27), ama-triplefins angakacwaningisisiswa (Tripterygiid 1), ama-*Lampanyctus alatus*, ama-*H.quadrimaculatus* kanye nama-*Umbrina ronchus* - wona athembele kakhulu esizalweni somfula. Kuzo zonke izindawo okwakufundelwa kuzo, kwakubonakala kunezikhathi ezahlukene zokuqoqa zalolo nalolo qembu elihlala esizalweni okwakubonakala kunezikhathi ezidlula ezinye kuleso naleso sezikhathi zonyaka. Lokhu kwakunqike esikhathini sonyaka salolo luhlobo okuyilona elingumakhonya.

Endaweni engunge isizalo somfula, amaqanda asemasha asesemazingeni okukhula futhi ebe ewuhlobo oluthembele esizalweni somfula ngokwempilo atholakala ethanda ukuba maningi kanti lawo asemadadlana nasasondele ukuba yizinhlanzi zangempela futhi ebe engathembele kakhulu lapha esizalweni somfula atholakala emaningi kakhlu. Amadlambi olwandle atholakala equkethe kakhulu amaqanda amadala asasondele ukuba abe yizinhlanzi ayengama-68% esamba sonke esaqoqwa, kanti amaqanda aseyizinhlanzi ezincane abonakala kakhulu esifundweni esathatha ubusuku nemini ngenkathi isizalo somfula sisavaliwe (50%). Ogwini lolwandle amaqanda ohlobo lwaselwandle angathembele esizalweni somfula ngokwempilo atholakala esesemazingeni aphansi ngokukhula (67% wesamba sonke).

Ngokwezinga imicikilisho kanye nokucwaninga ngokuqathanisa okuxubaxubene (Ukwehlukanisakanye nokumiswa) kwakhombisa ngokusobala ukubaluleka kwezimo ezithile zendawo ekwakheni indlela yokuqoqwa kwamaqanda ezinhlanzi alesi sifundo. Kanti-ke, nokuvumelana kobuningi bamaqanda kanye nokuhambisana kwezimo zendawo akhombisa ukuthi avuna uhlobo oluthile. Isimo esibalulekile esifakazela umkhondo owaqashelwa wamaqanda ezinhlanzi kwaba (ρ_w = 0.55 - ngokwezilinganiso zokuvumelana zikaSpearmans). Kanti-ke ukuqathaniswa kwezivumelwano kwezimo zendawo zonke ezazilinganisiwe kwakubalulekile ekutholeni umkhondo wobuningi (isib. ρ_w = 0.48 ubusawoti + ukudungeka, ρ_w = 0.41 wobusawothi + izinga lokushisa + ukudungeka).

Ukucwaningwa kokushintshana kwamaqanda ezinhlanzi ngenkathi yebuya lolwandle emachwebeni aseThekwini, eRichards Bay kanye nase St Lucia Estuary akhombisa ukuthi izinhlobo ezithile zebuya zisetshenziswa yizinhlobo ezithile njengesithuthi (isib. ama-Argyrosomus sp., ama-Pomadasys commersonnii kanye nama-Solea bleekeri), okusho ukuthi, ubuningi balezi zinhlobo babubonakala bubuningi ngezikhathi zebuya kanye nasekujuleni. ($P< 0.05$).

Sesiphetha, imiphumela yalesi sifundo ikhombise ngokusobala ukuthi kukhona izinhlobo ezahlukene neziguquguqukayo ekuqoqekeni kwamaqanda ezinhlanzi ezizalweni zemifula nasosebeni logu laKwaZulu-Natalali. Amaqanda, (ikakhulukazi lawo asevuthiwe) ahlobene nezinhlanzi zasesizalweni ayemaningi kuzo zozintathu lezi zizalo kanye namadlambi olwandle, okuchaza ukuthi lezi zindawo zisebenza njengezinkulisa zalezi zinhlobo. Kukhona nezifundo eziphathelene nohlobo

olukhethekile, oluphathelene namazinga okuzithokozisa kanye nokuhweba adingakalayo ukwenza izinqumo mayelana nokongiwa kanye nokusethenziswa kwalezo zinhlobo.

OPSOMMING

Hierdie studie fokus op die samestelling van vislarwe-groeperings in potensiële kweek-habitats ten einde lig te werp op die aanwasprosesse van visse in die Kwazulu-Natal streek. Hierdie samestelling, die mate van getyrivier-assosiasie van alle taksa, die tydelike en ruimtelike digtheidspatrone en die ontwikkelingstadiums van die vislarwes is ondersoek in drie groot getyrivier-sisteme, 'n brandersone en 'n post-breekwater mariene omgewing. Bykomend is daar twee 24 uur riviermondingstudies onderneem. Ten einde insig te verkry in die moontlike veroorsakende meganismes vir die waargenome digtheidspatrone is verwantskappe tussen digthede van vislarwes en omgewingsveranderlikes ondersoek.

Vislarwes is gemonster in Durbanhawe en Richardsbaaihawe. Monsters is by bo-, -middel en -bodem dieptes geneem in die baggerkanaal (100 tot 200 meter vanaf die hawe-ingang) oor 'n 13 en 12 maande studietydperk, onderskeidelik. Vislarwes van die St Lucia getyrivier is versamel oor 'n 12 maande tydperk by 'n permanente stasie, 4km vanaf die mond. 'n Totaal van 8797 vislarwes, verteenwoordigend van 64 families en 144 taksa, is versamel in Durbanhawe. In Richardsbaaihawe is, uit 'n totaal van 7163 vislarwes, 105 taksa, verteenwoordigend van 53 families, versamel. Larwes van die doring-ansjovis *Stolephorus holodon*, was volop in beide hawes (32% en 10% van die totale vangs, onderskeidelik), met die bloulintharing *Herklotsichthys quadrimaculatus* (30%) en 'n ongeïdentifiseerde dikkop Gobiid 12 (9%) dominant in beide Durbanhawe en Richardsbaaihawe, onderskeidelik. In die St.Lucia getyrivier is in totaal 51590 vislarwes versamel wat 85 taksa en 44 families verteenwoordig. Die rivier-dikkop *Glossogobius callidus* (67%) en die rivier-rondeharing *Gilchristella aestuaria* (19%) was die mees dominante spesies.

Vislarwes in die brandersone is maandeliks versamel by ses stasies, tot 3km noord van die St Lucia getyrivier-mond, met behulp van 'n stootnet. 'n 24 uur studie is ook onderneem in die brandersone terwyl die getyrivier-mond toe was. Meer vislarwes is tydens hierdie studie versamel as gedurende die hele 12 maande studie: 13731 en

2931 vislarwes onderskeidelik. Die samestelling van vislarwe-groeperings is gekarakteriseer deur taksa in die Sparidae, Haemulidae, Ambassidae, Tripterygiidae en Chanidae families. Die volopste spesies was *Pomadasys olivaceum, Ambassis* sp., *Rhabdosargus holubi, Croilia mossambica* en *Chanos chanos.* Vislarwes is ook gemonster in die aanliggende post-breekwater kussone; by vyf stasies in 'n transek tot 2.5km see-in en by twee stasies noord en suid van die St Lucia getyrivier-mond. Hierdie samesteling het bestaan uit 'n totaal van 6069 vislarwes verteenwoordigend van 246 taksa en 98 families. Larwes in die families Myctophidae en Tripterygiidae het onderskeidelik 21% en 16% van die totale vangs uitgemaak, met die dominante spesies 'n ongeïdentifiseerde drievin, Tripterygiid 1, en die lanternvis, *Benthosema fibulatum.*

Die persentasie bydra tot die totale vislarwe-vangs van getyrivier-geassosieerde visspesies het toegeneem vanaf die "getyrivier-habitat" (St Lucia) na die "semigetyrivier-habitat" (Richardsbaaihawe en die brandersone) tot die "mariene-habitat" (Durbanhawe en die post-breekwater kussone). Spesies verteenwoordigend van elke getyrivier-geassosieerde groep was byvoorbeeld: *G.aestuaria, Thryssa vitrirostris* en *Rhabdosargus* spp. - getyrivier-afhanklik; *S.holodon, C.mossambica* en *Ambassis* spp. - gedeeltelik getyrivier-afhanklik; ongeïdentifiseerde dikkoppe (Gobiid 12 en Gobiid 27), ongeïdentifiseerde driefin (Tripterygiid 1), *Lampanyctus alatus, H.quadrimaculatus* en *Umbrina ronchus* - getyrivier-onafhanklik. In al die studiegebiede is verskillende aanwasperiodes waargeneem vir elke getyrivier-assosiasie groep, met pieke in digthede in al vier seisoene. Dit was afhanklik van die seisoenaliteit van die dominante spesies wat teenwoordig was in 'n spesifieke studiegebied.

In die getyrivier-omgewings was die jong larwes van getyrivier-afhanklike spesies redelik volop, terwyl ouer larwes en vroeë vingerlinge van gedeeltelik getyrivier-afhanklike spesies in die meerderheid was. Die brandersone-habitat is gedomineer deur postfleksiese larwes (68% van die totale vangs) van getyrivier-geassosieerde spesies, met vroeë vingerlinge van getyrivier-onafhanklike spesies dominant tydens die 24 uur studie. In die post-breekwater kusomgewing is gevind dat getyrivier-onafhanklike mariene spesies hoofsaaklik in die prefleksiese en fleksiese ontwikkelingstadia was (67 % van totale vangste).

Stapsgewyse regressie en multiveranderlike statistiese analises (Klassifikassie en Ordonasie) het duidelik gedui op die belang van omgewingsfaktore

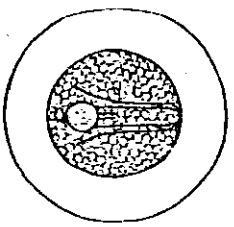
in die strukturering van die vislarwegroeperings. Verder is gevind dat die korrelasies tussen vislarwe-digthede en omgewingsveranderlikes spesiespesifiek is. Die belangrikste veranderlike wat verantwooordelik was vir die waargenome verspreidingspatrone was turbiditeit (ρ_w = 0.55). Die interkorrelasie tussen die waargenome omgewingsveranderlikes, was ook van belang in die bepaling van digtheidspatrone (b.v. ρ_w = 0.48 vir soutgehalte + troebelheid; ρ_w = 0.41 vir soutgehalte + temperatuur + troebelheid).

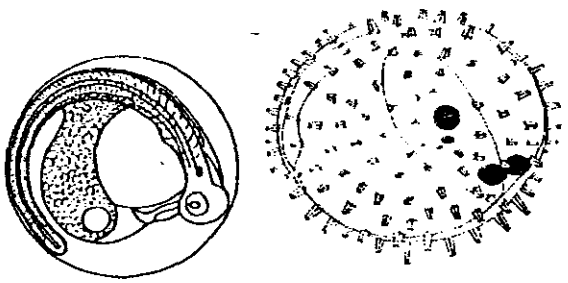
Analise van vislarwe-uitruiling tydens hoog- en laagwater in Durbanhawe, Richardsbaaihawe en St Lucia getyrivier-mond, het daarop gedui dat selektiewe getystroom vervoer 'n werwingsmeganisme is wat deur sekere spesies soos *Argyrosomus* sp., *Pomadasys commersonnii* en *Solea bleekeri* gebruik word. Vislarwe-digthede van hierdie spesies was beduidend hoër tydens hoogwater en in bodemwaters ($P < 0.05$).

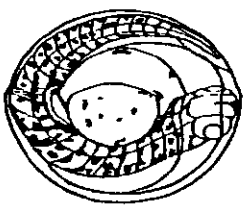
Uit die resultate is dit duidelik dat daar 'n diverse en dinamiese samesteling van vislarwe-groeperings in getyrivier- en kussisteme is, in Kwazulu-Natal. Vislarwes (hoofsaaklik postfleksies) van getyrivier-geassosieerde visspesies was volop in al drie getyrivier-sisteme en in die brandersone. Dit dui daarop dat hierdie setels as kweehabitats funksioneer vir hierdie spesies. Bykomende spesiespesifieke studies op die larwale stadiums van rekreasioneel en kommersieel belangrike lynvisse word benodig ten einde bestuursbesluite aangaande die bewaring en benutting van sulke spesies te maak.

CHAPTER 1

Introduction







1. INTRODUCTION

1.1 Rationale

The usefulness in studying the pelagic stage of estuarine fishes in recruitment studies is evident from the literature. The answers to vital questions in ecology and resource management regarding recruitment variability lie in understanding the pelagic stage (Doherty and Williams 1988). It is generally established that processes that control year-class strength occur early in the life history of most fish species (Miller 1988) thus, studies on larval rather than post-recruitment stages will elucidate processes limiting the abundance of fish populations (Jones 1991). The recruitment process occurs in nursery areas such as estuaries, surf zones and embayments of the nearshore marine environment in the early stages of their life cycle. This link is vital in the life cycles of a number of marine fish species that are dependent to some degree on nursery habitats. It is evident, therefore, that in assessing fish stocks of a particular coastal region it is necessary to study the assemblages of fish larvae occurring in all potential nursery areas for that region. Leis (1993) pointed out that it is best to study assemblages of larvae rather than individual species due to the complexity of early life history characteristics. A "fish assemblage" describes all fish species in a defined area irrespective of whether they interact or not (Wootton 1990). A knowledge of how individual species respond to abiotic and biotic environmental factors is required to understand the dynamics of a fish assemblage.

The present study was undertaken to elucidate the maintenance and recruitment of estuarine-associated fishes in the KwaZulu-Natal coastal region of South Africa by examining assemblages of fish larvae in potential nursery habitats. Only a few large estuarine systems occur along this coastline, in particular Durban Harbour, Richards Bay Harbour and the St. Lucia Estuary. The present study focuses on these three estuarine systems for the following reasons:

- Durban and Richards Bay Harbour have been shown to be important nursery sites for a number of juvenile marine fish species which normally occur in KwaZulu-Natal estuaries (Cyrus and Forbes 1994; Hay *et al.* 1995). Examination of the larval stages of these fish would further elucidate the nursery function of the harbours, and the recruitment processes of the fish.

- St Lucia is an estuarine-lake system which also functions as an important nursery site for many estuarine-associated fish species (Taylor 1982; Cyrus 1991). In addition, the St Lucia system has considerable conservation value (CSIR Environmental Services 1993) and hence warrants additional research. Investigation on the larval stages of the fish recruiting into the system would further clarify the systems function as a nursery site.

No studies on larval fish communities in the surf zone have been undertaken in KwaZulu-Natal but research has been undertaken in the Western and Eastern Cape which has indicated the importance of the surf zone habitat as a nursery site for certain fish species. Research on ichthyoplankton in nearshore coastal habitats has also only been undertaken in the Cape. All these habitats are potential nursery sites or transitory routes to nursery areas for estuarine-associated fishes and are, therefore, important to conserve and maintain. Cooper *et al.* (1995) concluded that the role of estuaries as large marine ecosystems on the KwaZulu-Natal coast is that they provide nursery areas for many juvenile marine fishes and must therefore be considered in any management decisions.

1.2 Background

Research on ichthyoplankton in South Africa was first undertaken in the Cape Peninsula coastal waters by Gilchrist (1903, 1904, 1916) followed by the more recent work of Brownell (1979). Intensive ichthyoplankton surveys have been done on the Benguela Current off the west coast (Olivar and Fortuno 1991; Olivar *et al.* 1992) and the Agulhas Current of the east coast (Beckley and van Ballegooyen 1992; Beckley and Hewitson 1994; Olivar and Beckley 1994a,b ; Beckley 1995) of South Africa. Studies on the early life history of fishes occurring in nursery areas have been undertaken in the Western and Eastern Cape in estuaries (Melville-Smith and Baird 1980; Melville-Smith 1981; Whitfield 1989a; Harrison and Whitfield 1990), estuary mouths/inlets (Melville-Smith *et al.* 1981; Beckley 1985a; Whitfield 1989b), nearshore coastal zones (Beckley 1986; Tilney and Buxton 1994), tidal pools (Beckley 1985b) and in the surf zone (Whitfield 1989c). No ichthyoplankton research on nursery areas has been undertaken on the KwaZulu-Natal

coast, with the exception of two studies in the St Lucia Estuary. The first study (Wallace 1975a) only gives a brief description of species composition and the second study (Martin *et al.* 1992) used a 1mm mesh net and thus, sampled mainly juveniles.

Research on estuarine fish populations in southern African has been directed primarily at the juvenile and adult life history stages (Wallace 1975a,b; Wallace and van der Elst 1975; Beckley 1983; 1984; Wallace *et al.* 1984; Bennett *et al.* 1985; Cyrus and Blaber 1987a,b; Whitfield 1988; Bennett 1989a; Whitfield and Kok 1992) with relatively little attention given to larval ecology. The use of these estuarine systems as nursery areas for the juvenile life history stage of fishes on the KwaZulu-Natal coast have been investigated and been found to have considerable value as nursery sites (Wallace and van der Elst 1975; Wallace *et al.* 1984; Cyrus and Martin 1991). The Richards Bay and Durban harbours are situated in the KwaZulu-Natal region and were originally natural estuarine systems which now function as important shipping ports. These systems still function as important estuarine nursery for many juvenile marine fishes, despite their development into harbours (Hay *et al.* 1995). The only plankton study done on these systems has been on postlarvae of penaied prawns by Forbes *et al.* (1994) which further emphasised the importance of these systems as nursery grounds for larvae of marine organisms. Oceanographic features associated with the shoreward edge of the Agulhas Current off the east coast are important in the dispersal and retention of marine fish larvae to inshore nursery habitats (Heydorn 1978a; Beckley 1995).

The ichthyoplankton found in estuaries can either result from spawning within the estuary or from early life history stage entering the estuary from the nearshore marine environment (de la Fontaine 1990). The different ways in which fish utilise estuaries have been categorised by various workers (McHugh 1967; Dando 1984; Wallace *et al.* 1984; Lenanton and Potter 1987; Loneragan *et al.* 1989; Potter *et al.* 1990; Neira *et al.* 1992). The majority of fishes found in estuaries are those species that spawn at sea, though there are a few species that complete their entire life cycle in estuaries (Haedrich 1983; Dando 1984; Claridge *et al.* 1986). The occurrence of marine species in estuaries tends to be either seasonal and in large numbers (marine estuarine-opportunists) or irregular and in small numbers (marine stragglers) (Lenanton and Potter 1987; Loneragan *et al.* 1989). The former consists mainly of species that utilise estuaries as nursery areas (Lenanton and

Potter 1987). Despite the fact that the above categories of life cycles for those fish which utilise estuaries are widely accepted, there have only been three studies which have quantified the relative contributions of adult, juvenile and larval fish species representing the different life cycle categories (Loneragan *et al.* 1989; Neira *et al.* 1992; Neira and Potter 1994). A decade ago, Wallace *et al.* (1984) divided the estuarine-associated fish fauna of southern Africa into six categories. Some modifications were made by Beckley (1985a) and by Whitfield (1994a; 1994b) who recently revised their classification system and recognises five major types of estuarine-dependence: estuarine species which breed in southern African estuaries; euryhaline marine species which usually breed at sea with the juveniles showing varying degrees of dependence; marine species which occur in estuaries in small numbers but are not dependent on them; euryhaline freshwater species; catadromous species.

The utilisation of the surf zone environment as a nursery area for juvenile and larval stages of fish has been investigated in the northern Gulf of Mexico (Modde 1980; Modde and Ross 1981; Ruple 1984), Japan (Senta and Kinoshita 1985; Kinoshita 1986; Kinoshita and Fujita 1988) and South Africa (Lasiak 1981, 1985; Bennett 1989b; Whitfield 1989c). Results from the study by Senta and Kinoshita (1985) showed that the ichthyoplankton assemblages of the surf zone differ from those of other biotopes, and vary over diel and seasonal periods. Certain species of juvenile fish have been shown to be entirely dependent on the surf zone as a nursery habitat (Lenanton 1982; Bennett 1989b). Only one study in South Africa has been done specifically on larval fish occurring in the surf zone (Whitfield 1989c) and was done adjacent to the Swartvlei Estuary in the Western Cape.

Boehlert and Mundy (1988) recognise the first phase of movement of larval fish, necessary for recruitment to estuaries by species spawned offshore, as being the accumulation of larvae in the nearshore coastal zone. Studies in the coastal zone along the east coast of the United States were undertaken to locate larvae of fish species abundant as juveniles in the estuaries of the region (Fahay 1974; Kendall and Walford 1979). From this work they have identified spawning times and seasons for many fish species in the region. Studies on ichthyoplankton assemblages of nearshore regions in South Africa have been undertaken in the Eastern Cape (Beckley 1986; Tilney and Buxton 1994) in relation to

coastal zone utilization by juvenile fishes. Estuarine orientation of fishes is dependent on swimming ability and the response of a species to the prevailing environmental conditions. These recruitment responses vary among species and between size and developmental stage (Whitfield *et al.* 1981; Whitfield 1994c)

The recruitment of species spawned offshore is a two-stage process which is dependent firstly upon factors in the offshore planktonic environment and secondly upon estuarine factors related to tidal flux in the mouth (Boehlert and Mundy 1988). Sampling studies in the mouths of estuaries have provided much information on the movements of larval and juvenile fishes through inlets. Understanding the mechanisms by which larvae enter and retain themselves within the estuary requires information on the diel movements of the larvae in the inlet of the estuary.

A comparison between the roles played by estuaries in the life-cycles of fishes in temperate Western Australia and temperate southern Africa showed there to be a greater penetration of subtropical/tropical fish taxa further southwards in Western Australia compared with southern Africa (Potter *et al.* 1990). This was attributed to differences in water temperature regimes i.e. the warm southward flowing Leeuwin Current off Western Australia transports tropical species into the temperate region. In southern Africa, the estuarine fish fauna on the KwaZulu-Natal and the Transkei coast is dominated by species typical of the subtropical and tropical Indo-Pacific fauna (Blaber 1981). Blaber (1981) suggested that environmental conditions, such as high turbidity and calm water conditions, influence the distribution of juvenile fish in Indo-Pacific estuaries. It thus seems that the composition of fish fauna in the estuarine habitats on the KwaZulu-Natal coast would be linked to the prevailing environmental conditions and the presence of major oceanic currents. Comparisons with similar studies on larval fish in other Indo-Pacific estuaries (e.g. Australia) will provide insight into the larval fish assemblage structure.

Multivariate analysis provides statistical methods for the study of joint relationships of variables in data that contain intercorrelations (James and McCulloch 1990). Comparisons of juvenile and adult fish assemblages, in different estuarine and coastal systems, have been made using multivariate classification and ordination techniques (Pollard 1994; Blaber *et al.* 1995). These studies correlated fish densities to abiotic factors and distinguished distinct assemblages in the different habitats, the

composition of which is influenced by prevailing environmental conditions. Larval fish studies have also employed classification and ordination techniques in order to understand assemblage structure (e.g. Leis 1993; Gray 1993). However, these larval fish studies did not correlate the observed abundance patterns to environmental conditions, such as water temperature, turbidity and salinity. Clarke and Warwick (1994) have recently developed a computer programme called PRIMER (Plymouth Routines in Multivariate Ecological Research) which enables the researcher to apply multivariate techniques, such as classification and ordination, in a "user friendly" manner. Included in the programme is a routine called BIO-ENV which links community data to environmental variables and determines the "best-fitting" variable/s responsible for producing those patterns. This technique is generally applied in pollution studies and, to my knowledge, has not been used in estuarine fish ecological studies.

1.3 Aims of Thesis

The present study investigated the recruitment of the early life history stages of fishes in the KwaZulu-Natal region and aimed to:

- Identify and describe the larval fish assemblages in potential nursery habitats
- Designate an estuarine-association category for each species and determine the relative contribution of each category to the larval assemblage
- Relate this to the role and importance of different coastal habitats as nursery areas
- Examine abundance and seasonality patterns and relate to the prevailing environmental factors
- Ascertain the relative importance of those environmental variables in influencing abundance patterns and therefore structuring the larval fish assemblages, with the use of multivariate techniques
- Compare assemblages in different types of estuarine habitats to gain insight into the forces structuring those communities
- Identify species dominating the assemblages and examine the species recruitment strategies

- Examine possible retention mechanisms in the mouth of an estuary
- Gain insight into the importance and hence conservation value/potential of these systems for management purposes

1.4 Thesis Outline

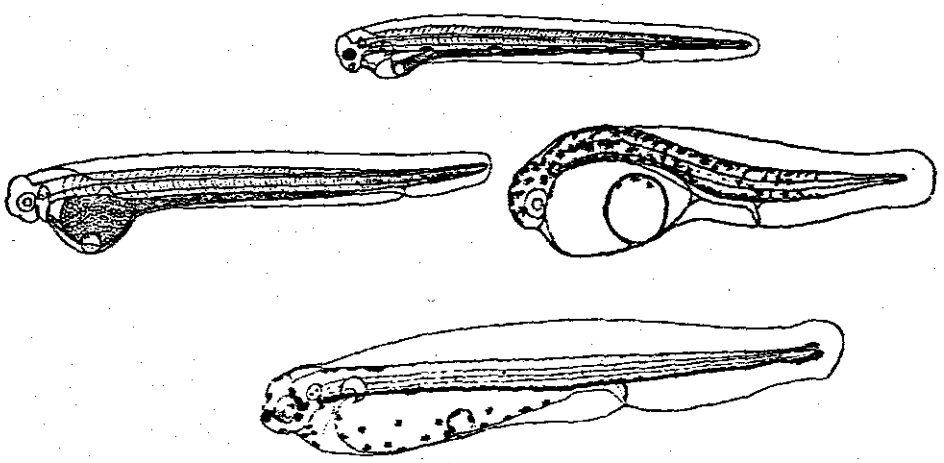
In brief, this thesis examines the composition, abundance, seasonality and developmental stages of the larval fish assemblages occurring in three large estuarine systems, a surf zone adjacent to an estuary and a nearshore zone off the mouth of an estuary. In addition, an inlet study was undertaken in the mouth of the St Lucia Estuary to ascertain recruitment mechanisms.

Chapters 2 and 3 details descriptions of each study area and the collection of fish larvae and laboratory procedures involved in the study. Chapters 4, 5 and 6 describe the larval fish assemblages in the three large estuarine systems: Durban Harbour, Richards Bay Harbour and St Lucia Estuary. A comparison of these three systems is made in Chapter 7 with the use of multivariate analysis. Chapter 8 investigates the role of the surf zone, adjacent to the St Lucia Estuary, as a habitat for larval fish which are en route to the estuarine environment. The larval fish assemblage in the nearshore coastal zone off the mouth of the St Lucia Estuary is examined in Chapter 9 and is followed by Chapter 10 which combines results from the St Lucia Estuary, surf zone and nearshore zone to gain insight into ocean-estuarine exchange mechanisms.

Finally, in Chapter 11 the significance of the findings of the present study and the importance of the estuarine and coastal habitats in KwaZulu-Natal as nursery sites, for estuarine-associated fish species, are discussed. The major points from each Chapter are discussed in a global context under five different topics. Recommendations for further research in larval fish studies is given, with special reference to estuarine and coastal systems in southern Africa.

CHAPTER 2

Description of Study Sites



2. DESCRIPTION OF STUDY SITES

2.1 Introduction

The estuaries of KwaZulu-Natal fall into a subtropical region between latitudes 26°S and 31°S (Figure 2.1), an area characterised by high summer rainfall but with periods of severe drought occurring approximately every 10 years (Dyer and Tyson 1977). Begg (1978) lists a total of 73 estuarine systems in KwaZulu-Natal the majority of which are "small" systems (average area < 25 km^2) with vastly different catchment areas for each estuarine system. For the purpose of the present study a definition of an estuarine system is "a partially enclosed body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity" (Day 1981b) and includes embayments which are subjected to tidal influences and salinities are essentially marine (Begg 1978). The present study focuses on three of the largest estuarine systems on the KwaZulu-Natal coast, the St Lucia Estuary, Richards Bay Harbour and Durban Harbour which together account for approximately 89% of total estuarine area in KwaZulu-Natal (Begg 1978). The catchment area for the St Lucia system is considerably larger than the other two systems (St Lucia - 8 982 km^2 compared with, say, Durban Harbour - 210 km^2, from Begg 1978) and is the largest estuarine system in southern Africa (Blaber 1985).

The ichthyofaunal composition of these subtropical estuaries has a relatively high species diversity since minimum water temperatures in the estuaries of KwaZulu-Natal are usually above 14°C (Whitfield 1994a). The extreme temporal variability in physico-chemical states of southern African estuaries (Day 1981b, c) affects the biotic processes (Whitfield and Wooldridge 1994) and hence the diversity and abundance of ichthyofauna occurring in these systems. Whitfield (1994b) describes the fishes of southern African estuaries has having a low speciation potential due to dominance of marine eurytopes and inhibition of estuarine stenotopes by widely fluctuating estuarine environments. Contributing to these naturally fluctuating conditions are man-made perturbations such as impoundments of rivers entering estuaries which reduces freshwater inflow (Whitfield and Wooldridge 1994), harbour development and bad agricultural practices in catchment areas. All three systems examined in the present study have been impacted upon in one way or another and detailed descriptions of each are given below.

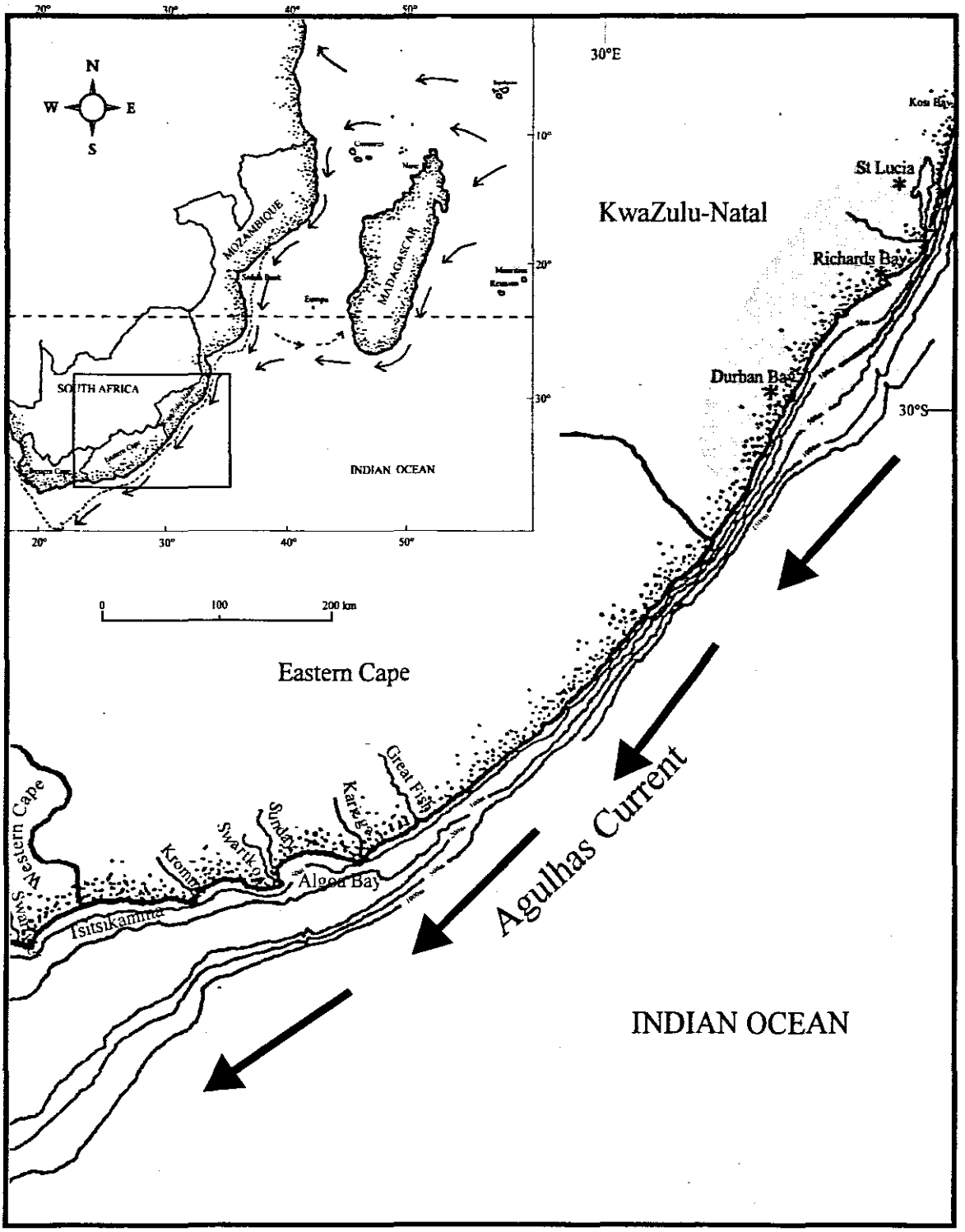


Figure 2.1. Map showing the KwaZulu-Natal region on the South African coast with the estuarine systems, examined in the present study, indicated by the shading: Durban Bay, Richards Bay and the St Lucia Estuary. Insert shows major ocean currents in the southern African region.

2.2 Durban Harbour

Durban Harbour is located at 29°53'S and 31°00'E in the KwaZulu-Natal region (Figure 2.1) and is referred to as an estuarine bay (Whitfield and Wooldridge 1994) since the system is subject to tidal influences and is essentially marine (Begg 1978). Prior to the development of the harbour, in the late 1800s, the system was called "Port Natal" and described as a large bay with freshwater flowing into it (Holden 1855). Port Natal was permanently open to the sea and shallow (< 3 m) with the depth being varied depending on the state of the sandbar in the entrance channel (Hay *et al.* 1995). Today, Durban Harbour is better defined as an "embayment" (Begg 1978) or as an "estuarine bay" (Whitfield and Wooldridge 1994) since the system is tidally dominated with near-marine salinities. Durban Bay must have originally functioned as a diverse and healthy estuarine ecosystem (Hay *et al.* 1995) and the first attempt to modify the configuration of Port Natal (as it was then known), to improve its function as a harbour began in the mid-1800's (Brakenbury 1991). A sand bar, which was situated at the mouth of the bay, was removed so that vessels could move freely into the bay (Figure 2.2A). Subsequent developments of the south breakwater and north pier were completed by 1893 and the depth of the harbour entrance was increased from 1.8 m to 3.3 m. (Begg 1978). Construction of wharfs and quays continued and Durban Harbour developed into its present day structure, functioning primarily as a shipping harbour (Figure 2.2B).

Two rivers, the Umbilo and Mhlatuzana, enter the bay through canalised inlets on the south west side of the harbour (Figure 2.2B). Little freshwater input occurs from these rivers, except during floods, resulting in essentially marine conditions (Forbes *et al.* 1994). The surface area of the bay is approximately 8 km^2 and has a maximum depth of 12 m with a shore line perimeter of ± 27 km (Begg 1978; Forbes *et al.* 1994). Over spring flood-tide periods, the amount of water entering the harbour (entrance = 230 m wide, Hay *et al.* 1993) was estimated to be 13.5 $m^3 \times 10^6$ (Forbes *et al.* 1994). Since the bay is a marine-dominated tidal system, the gradients in environmental conditions typical of estuaries do not occur. Continuing developments and increased pollution inputs and recreational activities have contributed to considerable degradation of Durban Bay and therefore its function as an estuarine habitat (Begg 1978; Guastella 1994; Hay *et al.* 1995).

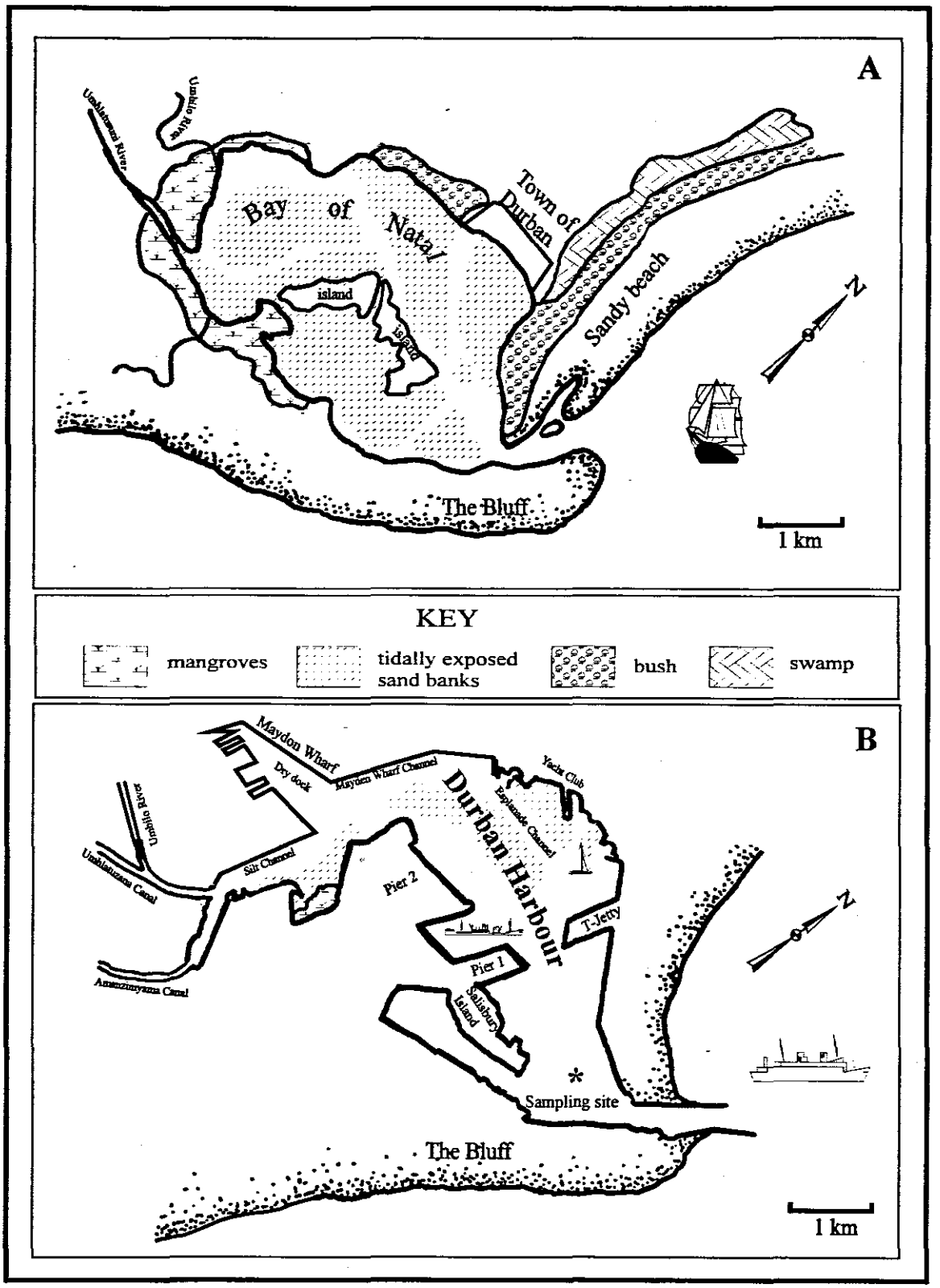


Figure 2.2. Durban Bay prior to harbour developments in the early 1850's (A) and Durban Harbour as it is today (B). (adapted from Hay et al. 1993)

2.3 Richards Bay Harbour

Richards Bay Harbour is situated at 28°49'S and 32°05'E on the KwaZulu-Natal coast (Figure 2.1) . Unlike Durban Bay, Richards Bay was only developed as a shipping port in the early 1970's (Brackenbury 1991) (Figure 2.3A) and was known as the Umhlatuzi Lagoon (Begg 1978). Early Portuguese navigators aptly called the estuary "Rio dos Peixos" meaning "river of many fishes" (Begg 1978) since the system functioned as a typical nursery and feeding ground for many marine fish species (Millard and Harrison 1954). The bay was shallow (± 0.9 m deep) with a muddy bottom and environmental conditions were essentially estuarine i.e. high turbidities and moderate salinity and temperature ranges (Grindley and Wooldridge 1974; Day 1981b). Harbour development commenced in 1970 and by 1974 a 4km berm across the bay separated a dredged deep water harbour section in the north from a sanctuary area in the south (Brackenbury 1991). The area of Richards Bay was estimated to be three times that of Durban Harbour (3000ha) (Heydorn 1978b).

Begg (1978) gives comprehensive descriptions of the pre- and post-harbour development on abiotic and biotic factors of Richards Bay. In summary, the estuary was divided into two sections, the harbour and the sanctuary by a berm wall (Figure 2.3B) and the original mouth dredged to a depth of 24 m (originally 4.5 m) with a width of 750m. This increased the tidal exchange of marine water with a concomitant increase in salinities and decrease in turbidities i.e. stabilising environmental conditions. A substantial decrease in marginal vegetation, for example, eelgrass beds (*Zostera capensis*) and mangroves (*Avicennia, Bruguiera, Rhizophora*) occurred when the Bay was first being developed (Begg 1978), however, a large mangrove area now exists in the southern part of the harbour (see Figure 2.3B). Hay *et al.* (1995) gives an apt description of the changes to Richards Bay: "the development of the Port of Richards Bay saw the conversion of a shallow, narrow-mouthed lagoon into a deep marine bay; an entirely new and physically different system had been created".

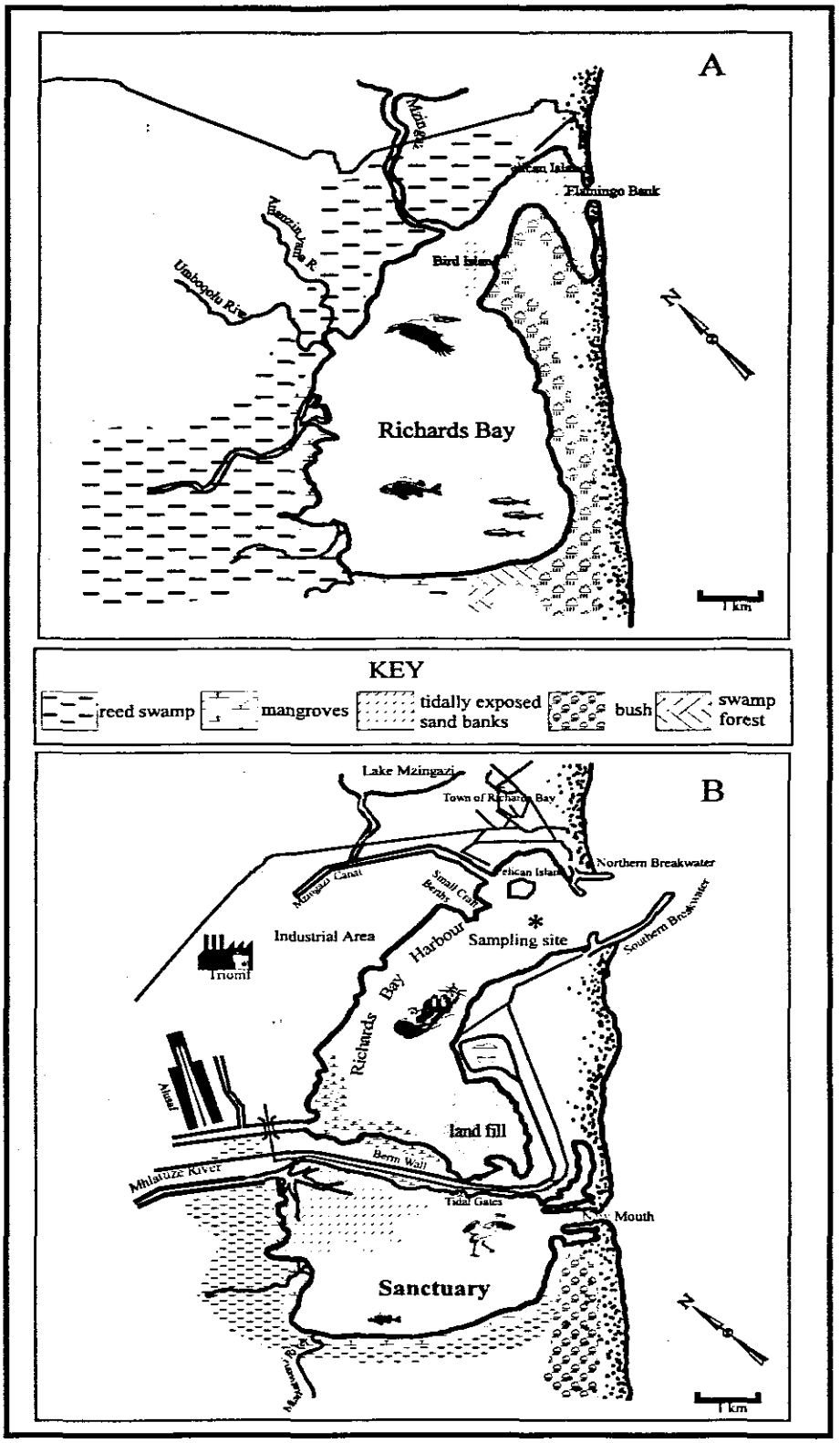


Figure 2.3. Richards Bay as it was before harbour development in 1964 (A) and Richards Bay Harbour as it is today (B). (adapted from Begg 1978)

2.4 St Lucia

2.4.1 Estuary

St Lucia is the largest estuarine system in southern Africa (Day 1981c) and is situated between 27°53'S to 28°23S and 32°21'E to 32°36'E on the KwaZulu-Natal coast (Figure 2.1). It should be referred to as an estuarine-linked lake system (Begg 1978) or estuarine lake (Whitfield and Wooldridge 1994) as it consists of two main parts, the estuary and adjoining 21 km entrance channel known as the Narrows, and the estuarine lake component (Cyrus 1991) (Figure 2.4). The whole system covers an area of 215 to 420 km^2 and an average depth of 1 to 2.5 m depending on water levels (Begg 1978; Day 1981c). The mean annual runoff in the catchment is estimated to be 287 x 10^6 m^3 and has a subtropical coastal and temperate climate (Wright and Mason 1993). Mid-latitude cyclonic activity is a dominant weather pattern in this region and in January 1984 extensive flooding of the St Lucia system occurred as a result of Cyclone Domoina and Cyclone Imboa. Evaporation is the most influential of the natural processes in St Lucia (Wright and Mason 1993) with an annual rate of 397 x 10^6 $m^{-3}.yr^{-1}$ which is greater than that of annual rainfall (268 x 10^6 $m^{-3}.yr^{-1}$) (Day 1981c). Four main rivers flow into the St Lucia lakes: Mkuze, Nyalazi, Mzinene and Hluhluwe Rivers, with a smaller river, the Mpate, entering the estuarine section (Figure 2.4).

Human interference during the past 50 years have drastically changed the St Lucia system (Wright and Mason 1993), particularly due to bad farming practices in the catchment resulting in high sedimentation rates (Begg 1978). Today, the principle use of the St Lucia system is recreational activities, particularly angling, but with the future threat of proposed mining activities on the eastern shores of the lakes (CSIR Environmental Services 1993).

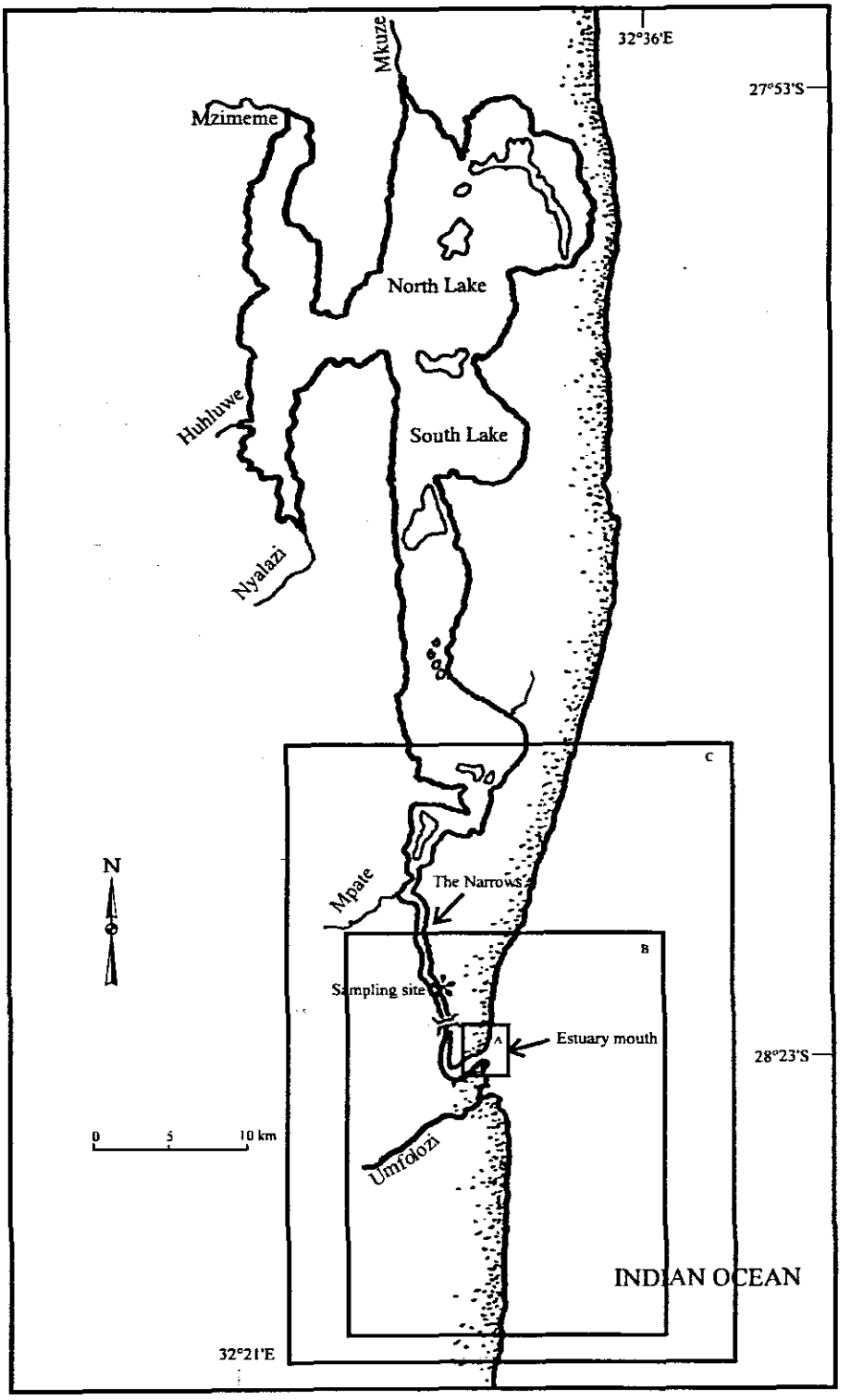


Figure 2.4. The St Lucia estuarine-linked lake system on the KwaZulu-Natal coast. Inserts show each of the study sites in the St Lucia region: (A) estuary mouth area - see Figure 2.5; (B) study area for surf zone study adjacent to the St Lucia Estuary mouth - see Figure 2.6; (C) nearshore coastal zone study area adjacent to St Lucia - see Figure 2.7.

2.4.2 Estuary mouth/inlet

The estuary mouth is extremely dynamic with a tidal inlet usually 75 to 150 m wide (Wright and Mason 1990) (Figure 2.5). Although the estuary mouth can close during low rainfall years it is kept open artificially (Day 1981c; Wright and Mason 1990) and hence can be classed as permanently open. The tidal inlet channel is characterised by flood and ebb dominated channels (Figure 2.5A) with current velocities on the bottom measuring 0.72 ms^{-1} on spring flood tides and 0.34ms^{-1} on spring ebb tides. The inlet is therefore flood-tidally dominated (Wright and Mason 1990). The presence of a northern and southern spit at the estuary mouth (Figure 2.5A) indicates that longshore drift moves sediment into the estuary mouth from both directions i.e. gradual encroachment of marine-derived sediment into the estuary supports that fact that the inlet is flood-dominated (Wright and Mason 1993).

2.4.3 Surf zone

The surf zone adjacent to the St Lucia Estuary mouth is influenced by swells in the nearshore zone which are predominantly from the southeast, hence a northerly longshore surf zone current prevails (Begg 1978; Wright and Mason 1990) (Figure 2.6). The KwaZulu-Natal coastline has a particularly high energy surf zone with wave heights generally between 0.5 and 2.5 m throughout the year (Rossouw 1984).). However, if a northerly wind blows a longshore drift current of up to 1.7 ms^{-1} towards the south can occur (Wright 1990).

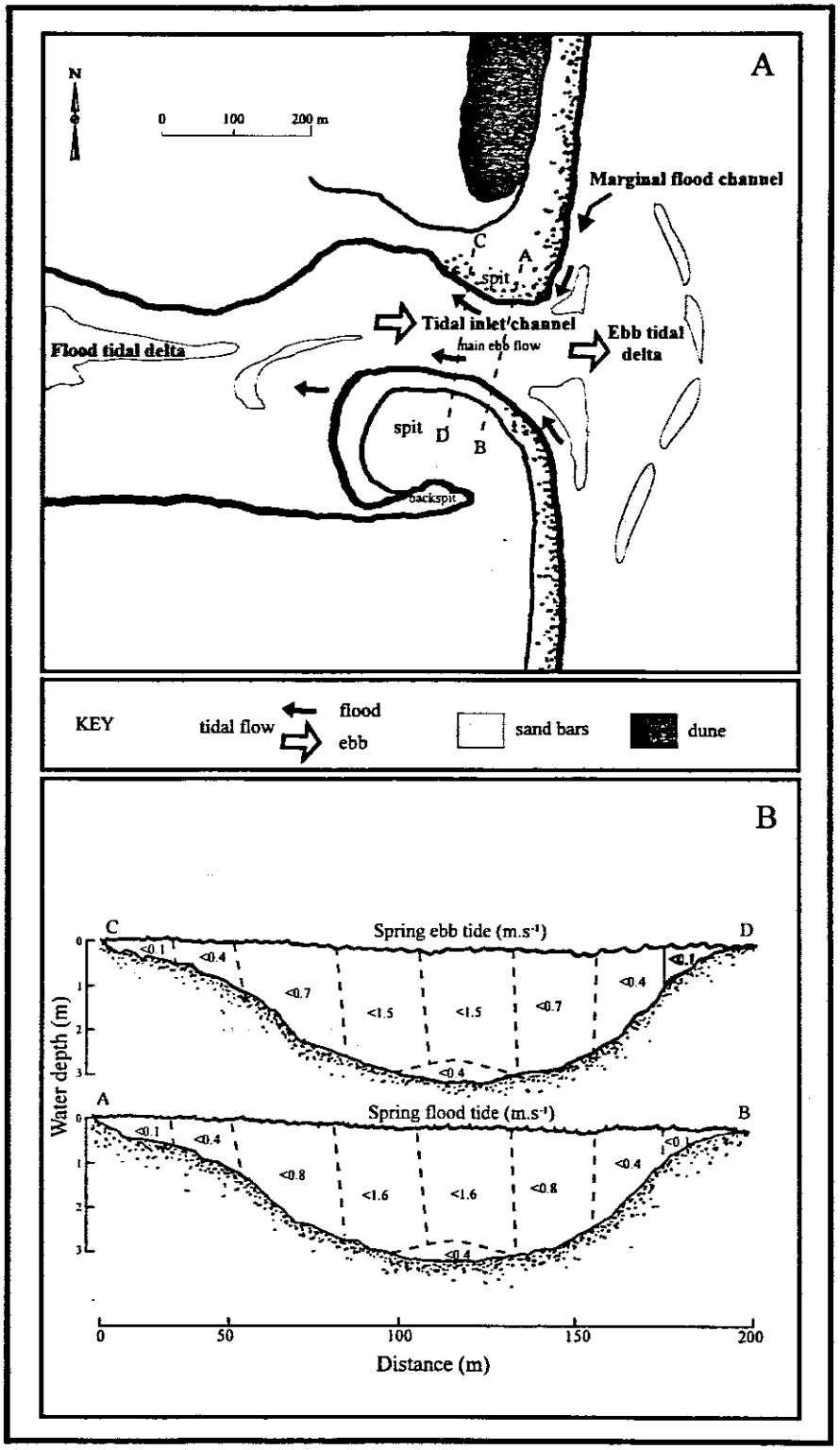


Figure 2.5. The configuration of the St Lucia Estuary mouth with ebb and flood tidal deltas present (A - adapted from Wright and Mason 1990). A current profile across the width of the mouth on a spring flood tide (A - B transect) and a spring ebb tide (C -D transect) is shown in (B), where values represent current speed ($m.s^{-1}$).

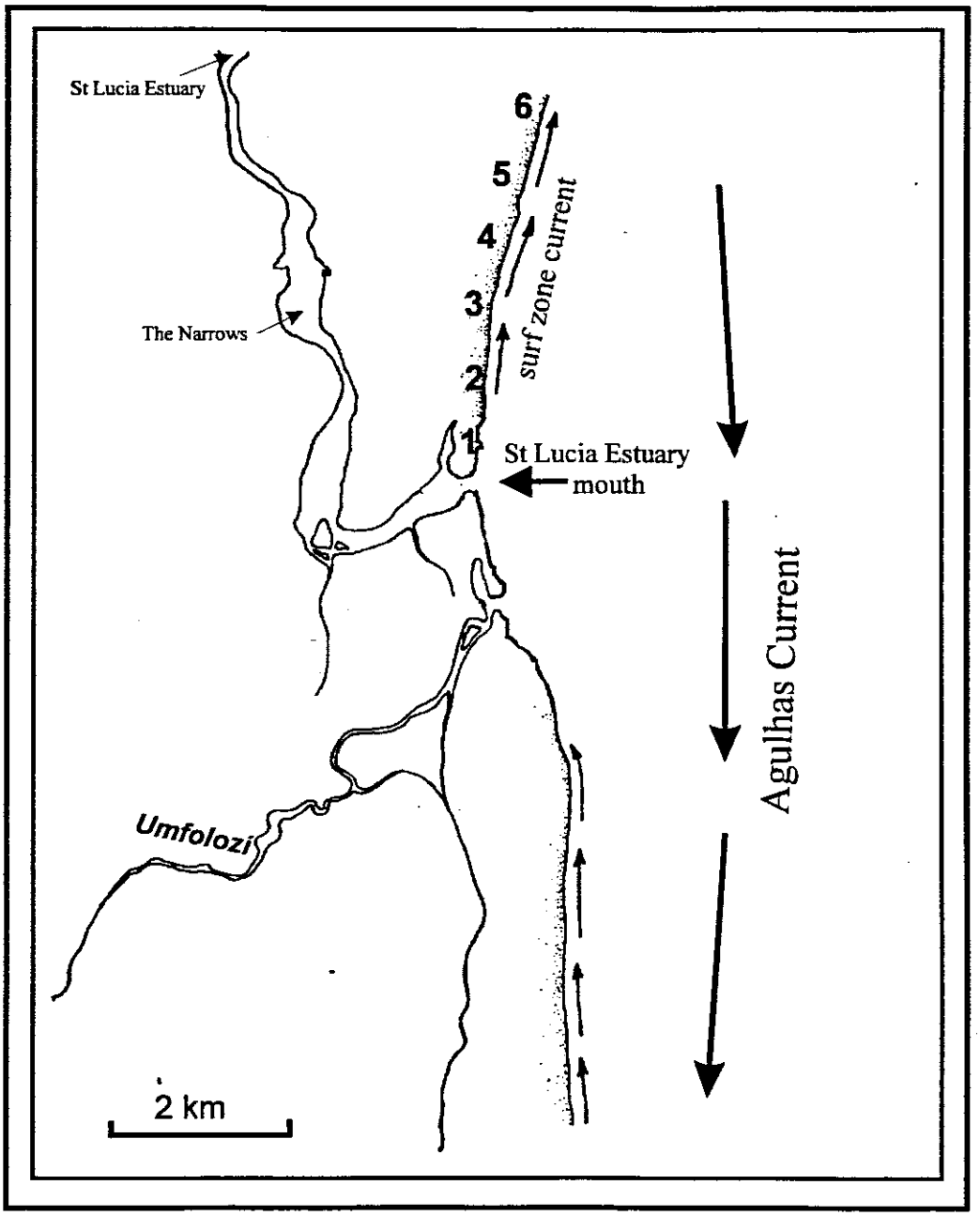


Figure 2.6. Location of surf zone study area adjacent to the St Lucia Estuary mouth. Stations 1 to 6 are indicated north from the Estuary mouth. Note location of the Umfolozi River mouth approximately 1 km south of the St Lucia Estuary mouth.

2.4.4 Nearshore Coastal Zone

The continental shelf north of Cape St Lucia is narrower than 10 km in places (Schumann 1988) and off the mouth of the St Lucia Estuary itself, the shelf break occurs at approximately 7 km offshore at the 100 m depth contour (Figure 2.7). The south-flowing Agulhas Current is a large-scale western boundary current which is established between 25 and 30°S (Pearce 1977) and, since it flows along the shelf break it has a dominant influence on the adjacent nearshore coastal zone (Martin and Flemming 1988; Schumann 1988). Since the shelf is narrow, tidal currents are generally small and wind-driven currents dominate the inshore shelf region (Pearce 1977) but are superimposed by shoreward intrusions of Agulhas Current surface water (Beckley and van Ballegooyen 1992). Cross-shelf flow appears to be onshore in the lower half of the water column, with an offshore compensatory flow in the upper layer (Schumann 1988). Off the Mfolozi/St Lucia river confluence these areas are probably frequently occupied by closed eddy systems (Flemming and Hay 1988). The regular alternation of north-easterly and south-westerly winds on the KwaZulu-Natal coast has a strong influence on the coastal waters in the region (Heydorn 1978a). Turbidity of inshore waters is increased substantially during the summer months when river outflow is increased, particularly in the St Lucia region.

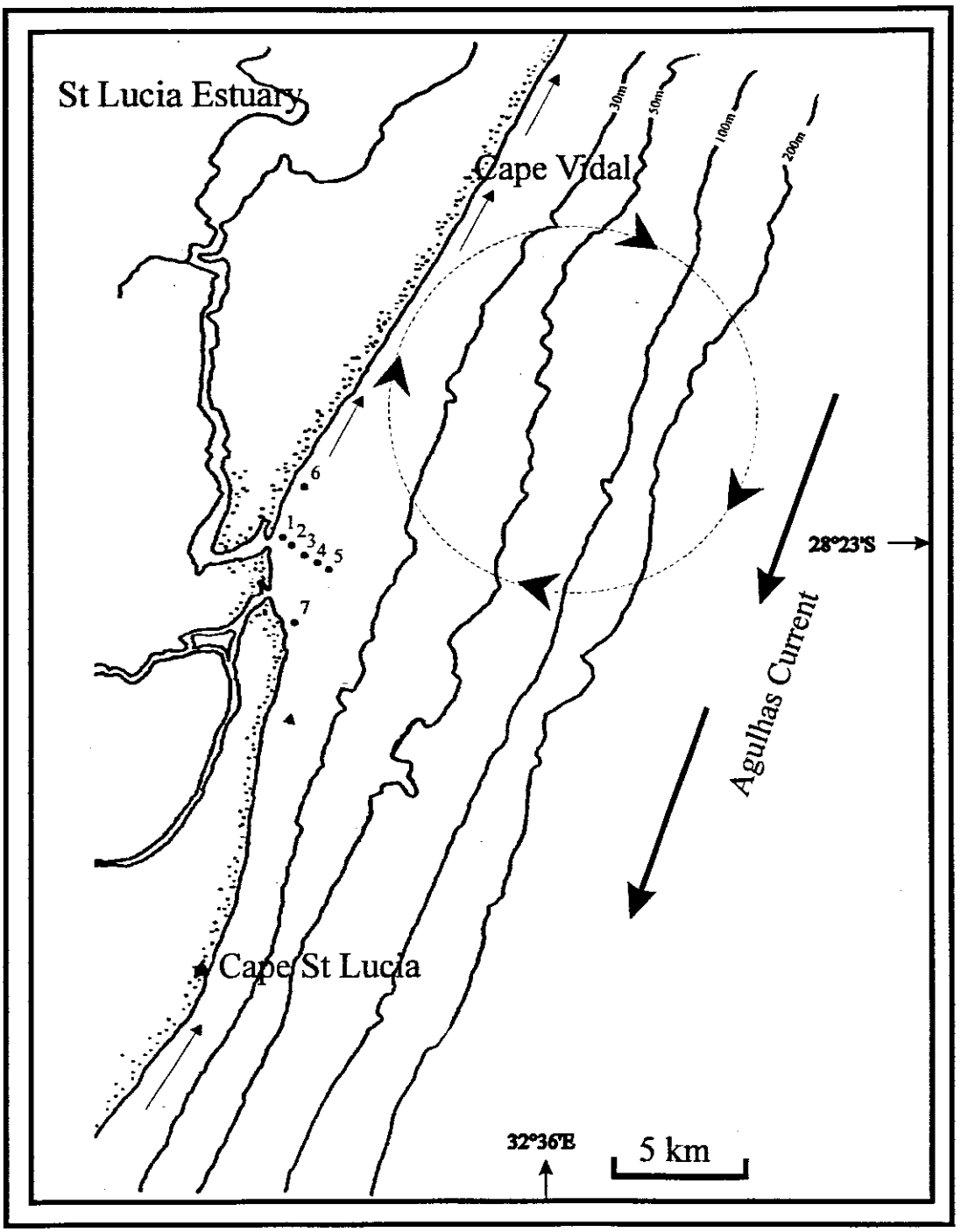
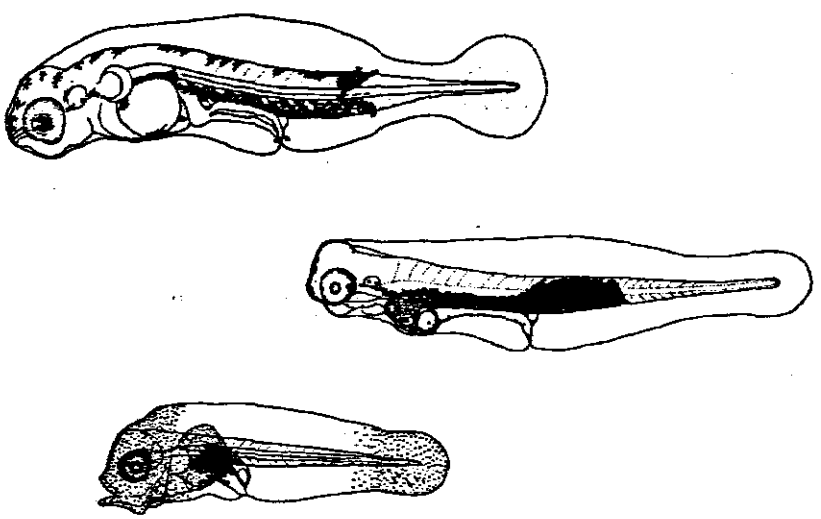


Figure 2.7. The nearshore coastal zone in the shelf waters of the St Lucia area with the current systems (closed eddies and the Agulhas Current) influencing this coastal region is indicated by arrows. Note sampling stations 1 to 5 in a transect directly in line with the Estuary mouth, and station 6 and 7 north and south of the mouth, respectively.

CHAPTER 3

Materials and Methods



3. MATERIALS AND METHODS

3.1. Collection of Fish Larvae

3.1.1. Durban Harbour and Richards Bay Harbour

At both Durban Harbour and Richards Bay Harbour, ichthyoplankton samples were collected at a sampling site in the dredged channel approximately 100 to 200m from the harbour entrance (Figures 2.2B and 2.3B, Chapter 2). Table 3.1 summarises the details of the sampling procedure for both harbours.

Table 3.1. Summary of sampling programmes for Durban Harbour and Richards Bay Harbour.

Sampling Programme	Durban Harbour	Richards Bay Harbour
Sampling dates (spring tide)	June 1991 to December 1992	June 1991 to November 1992
Total sampling trips	13	12
Mean (±SD) sampling depths (m)		
Mid	3.7±1.4	6.8±1.6
Bottom	8.5±2.5	12.5±1.6
Number of samples ($T_{1,2,3}$; $M_{1,2,3}$; $B_{1,2,3}$)[A]		
Ebb tide	110	106
Flood tide	119	102
Total	229	208
Mean (±SD) sample volumes (m^3)		
Top	108.0±33.5	128.9±38.1
Mid	113.8±35.4	135.4±30.2
Bottom	106.1±33.8	130.2±35.5

[A]a set of 3 samples at each depth for each tide.

A plankton net (500 µm, 57 cm diameter mouth, 2.5 m long), with a flow meter (General Oceanics), was towed behind a launch at an average speed of 1 $m.s^{-1}$. The net was mounted on a gimbal system so that it remained at right angles to the current, and a combination of a weight and either one or two floats allowed the net to be set at surface, mid and at near bottom depths. The depths of the mid and bottom samples varied depending on the state of the tide.

Samples were collected at night on consecutive ebb and flood tides per sampling trip. During some of the sampling trips fewer samples were collected due to technical problems. Temperature (°C), salinity (‰) and turbidity (NTU, Nephelometric Turbidity Units) were measured during the collection of each sample.

3.1.2. St Lucia

3.1.2.1 Estuary

Ichthyoplankton samples were taken at a fixed station midstream in the Narrows of the St Lucia Estuary approximately 4 km from the mouth (Figure 2.4, Chapter 2). Samples were collected over 13 successive full-moon spring tides from November 1987 to October 1988. It should be noted that in May 1988 there was a full-moon on the 1st and the 31st of the month and hence two sets of samples were collected for May (May_1 and May_2). A plankton net (500 µm, 57 cm diameter mouth, 2.5 m long), with a flow meter (General Oceanics), was deployed during flood tides behind an anchored boat. The net was mounted on a gimbal system so that it remained at right angles to the current. A combination of a weight and either one or two floats allowed the net to be set at the surface or at the bottom. The depth at the sampling station ranged from 2.6 to 3.6 m during the study.

Samples were taken on three consecutive nights over spring flood tides at approximately hourly intervals depending on the flood tide period and the strength of the tidal current. Each sample consisted of a 10 min surface set followed immediately by a 5 or 10 min bottom set (4 top and 4 bottom samples per night). Mean top and bottom sample volumes were 71.5 m^3 (SD = 24.9; n = 156) and 56.1 m^3 (SD = 22.7; n = 156), respectively. Temperature (°C), salinity (‰) and turbidity (NTU) were measured during

the collection of each sample. Current velocity (ms^{-1}) was also measured, but only from May to October 1988 since no current meter was available for the first half of the study.

3.1.2.2 Estuary mouth/inlet

Two 24-h sampling sessions, during February and March 1994, were undertaken in the mouth of the St Lucia Estuary (see Figure 2.5A, Chapter 2). A current profile across the width of the mouth is shown in Figure 2.5B: cross sections of transects A-B and C-D (Figure 2.5A) are current profiles of the spring flood tide and spring ebb tide during the February 24-h sampling session. Current velocities were measured using a flow meter (General Oceanics), at different depth intervals across the width of the entrance channel.

Replicate ichthyoplankton samples were collected in the middle of the inlet channel and at the edge of the channel (Figure 2.5A, Chapter 2) at approximately 90-min intervals for a period of 24-h. The total number of samples = 128 i.e. four tidal periods (day flood, night ebb, day ebb, night ebb) with eight samples (4 replicates) during each tidal period = 64 samples at both the mid-channel and edge sites.

For the mid-channel samples a plankton net (500 µm, 57 cm diameter mouth, 2.5 m long), with a flow meter (General Oceanics), was deployed during flood and ebb tides behind a small ski boat. The boat was not anchored since both flood and ebb tidal currents were too strong and the boat was therefore just directed into the oncoming current with the motors running. The edge samples were collected using a push net (1.5 x 0.3 m rectangular opening, 500 µm mesh net), equipped with a flow meter (General Oceanics), was held by two people into the flow of the oncoming tide. Mean volumes for flood and ebb tides at the mid-channel site were 89.6 m^3 (SD = 31.2) and 86.8 m^3 (SD = 46.9), respectively, and at the edge site they were 28.2 m^3 (SD = 12.5) and 48.2 m^3 (SD = 21.3), respectively. Current velocity (ms^{-1}), temperature (°C), salinity (‰) and turbidity (NTU) were measured at each time interval, but only at the mid-channel site.

3.1.2.3 Surf Zone

Early-stage fish were collected at six stations situated at approximately 500 m intervals north from the St Lucia Estuary mouth i.e. station 1 was at the mouth and station 6 was 3 km north of the mouth (Figure 2.6, Chapter 2). A "pushnet" (1.0 x 0.6 m rectangular opening, 500 µm mesh net), equipped with a flow meter (General Oceanics), was pulled by two people through the inner surf zone for approximately 5 to 10 min depending on the state of the wave action (mean volume sampled = 58.8 ± 13.2 m^3, total samples = 144). Samples were collected monthly from February 1992 to January 1993 on corresponding day and night spring low tides (full moon), at each of the six stations. Sampling could only be undertaken during low tide because of rough wave conditions at high tide. Temperature (°C), salinity (‰) and turbidity (NTU) were measured concurrently with each sample.

In February 1993, the estuary mouth had been closed since December 1992 and so a 24-h study was undertaken in the surf zone opposite the sand bar blocking the mouth of the estuary. Replicate samples were taken hourly at spring low tide during the day and night (once again samples could not be taken at high tide). Mean volume sampled was 31.8 ± 10.9 m^3 (total samples = 22).

3.1.2.4 Nearshore Coastal Zone

Samples were collected monthly over two days, during daylight hours only, from July 1990 to June 1991 on spring tides (full moon). No samples were taken in May 1991 due to adverse weather conditions. Each month, samples were taken from seven stations in the nearshore zone off the St Lucia Estuary mouth (Figure 2.7, Chapter 2). For each month sampled, stations 1 to 5 were sampled on day one - each station being 500 m apart and situated in a transect perpendicular to the coast directly in line with the estuary mouth. On day two of that month, stations 1 and 4 were sampled again in addition to station 6 (3 km north of estuary mouth and 500 m offshore) and station 7 (4 km south of the estuary mouth and 500m offshore). Replicate top and bottom samples were taken at each station using a plankton net (500 µm mesh, 57 cm diameter), equipped with a flow

meter (General Oceanics), which was towed behind a small ski boat. A combination of a weight and either one or two floats allowed the net to be set at the surface or at the bottom. Temperature (°C), salinity (‰) and turbidity (NTU) were measured during the collection of each set of replicate samples. The mean volume sampled and mean depth, in top and bottom samples, at each station is summarised in Table 3.2.

Table 3.2. Summary of sample volumes at top and bottom depths and at each station in the nearshore zone of St Lucia. (n, number of samples; vol, volume)

Station (km offshore)	Top		Bottom		
	n	vol (±1SD) (m^3)	n	vol (±1SD)	mean depth (m)
Station 1 (0.5 km)	44	87.9±14.5	44	128.6±47.1	10.9±1.6
Station 6 (0.5 km)	22	89.8±10.8	22	135.2±44.8	11.6±1.6
Station 7 (0.5 km)	22	91.3±12.5	22	141.9±52.7	11.4±1.3
Station 2 (1.0 km)	22	88.6±19.3	22	120.6±52.2	16.4±1.9
Station 3(1.5 km)	22	86.3±20.0	22	100.4±37.3	20.3±1.8
Station 4 (2.0 km)	44	103.3±70.9	44	121.9±64.0	22.2±2.5
Station 5 (2.5 km)	22	88.1±35.3	22	104.±23.9	28.0±1.2

3.2. Laboratory Procedures

3.2.1. Sorting and Identification of Fish Larvae

Ichthyoplankton samples were preserved in the field with 4% buffered formaldehyde. In the laboratory the fish larvae were sorted with the aid of a low-power stereo-microscope. Larvae were identified to the lowest possible taxon, using the criteria of Fahay (1983), Leis and Rennis (1983), Moser *et al.* (1984), Smith and Heemstra (1986), Okiyama (1988) and Leis and Trnski (1989). Fish body lengths (notochord length in preflexion and flexion larvae and standard length in postflexion larvae, Leis and Trnski 1989) were measured using an eyepiece micrometer for larvae <10 mm and vernier calipers for larger individuals. The term "fish larva" was used to designate that stage in the life history from hatching to attainment of complete fin ray counts and beginning of squamation, at which stage the fish becomes a juvenile (Kendall *et al.* 1984). Terminology to designate developmental larval stages follow Kendall *et al.* (1984): leptocephalus (Le), preflexion (Pr), flexion (Fl), postflexion (Po) and juvenile (Ju). Old larvae are defined as postflexion and young larvae as preflexion (Leis 1991). In the present study, flexion stages are included as young larvae.

(see Appendix I for a summary of all taxa identified in the present study, from all study sites. Presence or absence at a particular study site is noted by a +)

3.2.2. Analyses of Data

In all statistical analyses a significance level of $p < 0.05$ was used. All larval density data were log transformed [$\log_{10}(x + 1)$] to conform to normality and homogeneity of variances, and then tested for normality. Where necessary, turbidity and salinity data were also log transformed. Depending on the sampling regime for each study site, differences in environmental variables (current velocity, salinity, temperature and turbidity) and densities of fish larvae between different depths (top, mid and bottom - Durban and Richards Bay Harbours; top and bottom - St Lucia Estuary and nearshore zone), different times (day and night - surf zone) and between sampling dates were tested

for significance using a two-way or three-way analysis of variance (ANOVA - Tukey test). Duncans Multiple Range test was used to identify where significant differences occurred.

In Chapters 4, 5, 6, 8 and 9 multiple linear and stepwise-regressions were used to ascertain whether larval fish densities showed any statistical relationship with the environmental variables. In Chapters 7 and 10 multivariate analyses using classification and ordination are used to examine correlations between biotic and abiotic factors and are described in detail in section 7.2 (Chapter 7) and section 10.2.1 (Chapter 10).

In all studies, the total number of larvae for all taxa caught in all the samples was recorded and converted to a density (number of larvae per $100m^3$). These adjusted numbers were used to calculate the percentage contribution of each species to the total catch. The total mean catch (Tables 4.1, 5.1, 6.1, 8.1 and 9.1, in their respective Chapters) is the sum of the mean densities each month divided by the number of sampling periods.

3.2.3. Estuarine-Association Categories

For the purpose of the present study the term "estuarine-dependent" refers to those fish species for which estuaries form an essential habitat for at least one stage of the life cycle (Blaber *et al.* 1989). Each taxon was categorised according to what degree the species, in the southern African region, is dependent on estuaries in their life cycle. All taxa were then grouped into one of the following three groups (adapted from Whitfield 1994a,b): Note: the Australian equivalent is indicated in parentheses (Neira *et al.* 1992). Most of the unidentified goby specimens were designated as estuarine-independent taxa since they were either absent or not abundant in the estuarine environment (see Appendix I).

- **Estuarine-dependent taxa (estuarine - E)**

  Ia. Estuarine species which only breed in estuaries. e.g. the estuarine roundherring *Gilchristella aestuaria.*

IIa. Euryhaline marine species which usually breed at sea but the juveniles are dependent on estuaries as nursery areas. e.g. ladyfish *Elops machnata*

Va. Obligate catadromous species which require a freshwater phase in their development. e.g. longfin eel *Anguilla mossambica*

- **Partially estuarine-dependent taxa (marine-estuarine opportunists - O)**

  Ib. Estuarine species which breed in estuaries and the marine or freshwater environment. e.g. the river goby *Glossogobius callidus* and longsnout pipefish *Syngnathus acus.*

  IIb. Euryhaline marine species which usually breed at sea with the juveniles occurring in estuaries but are also found at sea. e.g. groovy mullet *Liza dumerilii.*

  IIc. Euryhaline marine species which usually breed at sea with the juveniles occurring in estuaries but are more abundant at sea. e.g. thorny anchovy *Stolephorus holodon.*

  Vb. Facultative catadromous species which do not require a freshwater phase in their development. e.g. oxeye tarpon *Megalops cyprinoides.*

- **Estuarine-independent taxa (marine stragglers - excl. the freshwater taxa - S)**

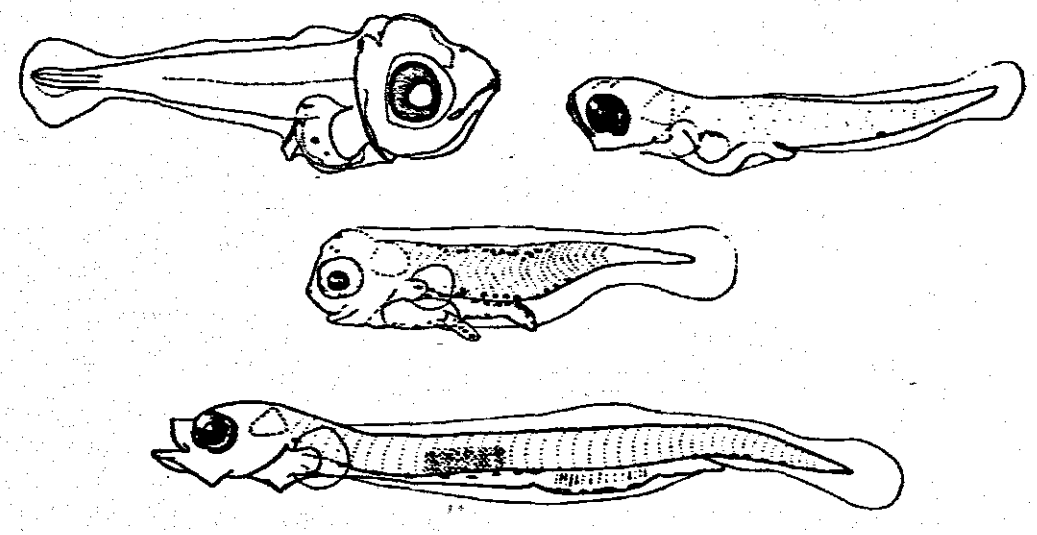
  IV. Euryhaline freshwater species. e.g. barebreast goby *Silhouettea sibayi.*

  IIIa. Marine species which occur in estuaries in small numbers but are not dependent on them - includes shore- and reef-associated neritic taxa e.g. piggy *Pomadasys olivaceum* and queenfish *Scomberoides* spp..

  IIIb. Marine species which occur in estuaries in small numbers but are not dependent on them - includes oceanic taxa (epi-, meso- and bathypelagic) e.g. lanternfish *Diaphus* spp. and lightfishes *Vinciguerria* spp.

CHAPTER 4

The Larval Fish Assemblage in Durban Harbour



4. THE LARVAL FISH ASSEMBLAGE IN DURBAN HARBOUR

4.1. Introduction

Durban Harbour is situated at 29°53'S and 31°00E on the KwaZulu-Natal coast (see Figure 2.1, Chapter 2) and is one of the busiest shipping ports in Africa. The harbour also functions as an important recreational angling venue since popular angling fish species, such as grunter and springer, predominate in the system (Guastella 1994). Port Philip Bay in Victoria, Australia, similarly functions as a shipping port and supports a significant commercial and amateur fishery (Jenkins 1986). An analysis of the eggs and larval stages of the fish in Port Philip Bay showed that larvae of two important commercial species, yellow-eyed mullet (*Aldrichetta forsteri*) and King George whiting (*Sillaginodes punctatus*) were rare or absent but were abundant as early juveniles (Jenkins 1986). Although there is a limited amount of information on ichthyoplankton in shipping ports these systems are usually modified estuaries and/or bays and, therefore, comparable.

Early biological surveys of the bay (Day and Morgans 1956; Wallace 1975a,b) found that despite the impact of the harbours development a surprisingly rich ichthyofauna persisted with many of the fish being euryhaline estuarine species typical of other KwaZulu-Natal estuaries. More recent studies still indicate that, despite the stenohaline marine component being prevalent, many of the fish species found in the bay are euryhaline estuarine species (Hay *et al.* 1993; Beckley *et al.* 1994; Cyrus and Forbes 1994; Graham 1994; Guastella 1994). These studies indicated that Durban Harbour still serves as an important nursery site for these fish species. All previous fish surveys have only examined adult and juvenile life history stages (Day and Morgans 1956; Wallace 1975a,b; Begg 1978; Hay et al. 1993; Beckley *et al.* 1994; Cyrus and Forbes 1994; Guastella 1994). No studies on the larval life history stages having been undertaken, with the exception of some non-quantitative work by A. D. Connell (pers. comm.[1]).

[1] Dr A. D. Connell, CSIR , Durban

To further our understanding of the utilisation of estuarine nursery areas by estuarine-associated fish species it is important to examine the early life history stages of those fish (Whitfield 1989a). Studies on larval fish assemblages in estuaries have shown that marine fish species which utilise estuaries as nurseries are recruited at an early life history stage, particularly during the postflexion larval developmental stage (Melville-Smith and Baird 1980; Miskiewicz 1987; Whitfield 1989a,b,c; Gaughan *et al.* 1990; Harrison and Whitfield 1990; Tzeng and Wang 1992; Neira *et al.* 1992; Neira and Potter 1994; Warlen 1994; Whitfield 1994c; Harris and Cyrus 1995a - see Chapter 6). This section of the present study investigated the composition, abundance, seasonality and developmental stages of larval fish occurring in Durban Harbour. Estuarine-associated taxa were identified and discussed in terms of recruitment into Durban Harbour. The following questions are addressed:

- what is the larval fish assemblage composition ?
- how is this related to the environmental conditions ?
- what proportion of species present are associated with estuaries ?
- are there any seasonal patterns in abundance ?
- at what developmental stage are the marine fish species, which utilise the harbour as a nursery site, recruiting at ?
- do the larvae utilise tidal currents as a recruitment mechanisms ?

4.2 Results

4.2.1 Environmental Variables

During the period June 1991 to December 1992 water conditions at the sample site in Durban Harbour were essentially marine. The mean monthly salinity reached a minimum of 34.0 ‰ in June and late October 1991, and a maximum of 35.0 ‰ in July 1991 and from May to December 1992 (Figure 4.1). No significant differences in salinities were found between ebb and flood tides ($F = 1.79$; $P = 0.18$) or with depth ($F = 1.44$; $P = 0.24$), but significant differences were found between sampling dates ($F = 32.50$; $P < 0.0001$).

Mean monthly water temperature reached a maximum of 24.3°C in December 1991 (Figure 4.1) and was lowest in July 1991 (19.2°C) and June 1992 (20.0°C). Temperatures were not significantly different between ebb and flood tides ($F = 0.01$; $P = 0.91$) but were significantly higher at surface and mid depths than at bottom depths ($F = 16.04$; $P < 0.0001$), and differed significantly between seasons ($F = 316.45$; $P < 0.0001$).

Monthly variations in water turbidity occurred with a maximum of 10.2 NTU in January 1992 and a minimum of 1.0 NTU in August 1992 (Figure 4.1). Turbidity was significantly higher on ebb tides ($F = 4.37$; $P = 0.04$) and was usually higher in bottom and mid water depths although this was not significant ($F = 2.10$; $P = 0.13$). Like salinity and temperature, the overall range in turbidities was not great but mean turbidities were significantly different between sampling periods ($F = 18.54$; $P < 0.0001$).

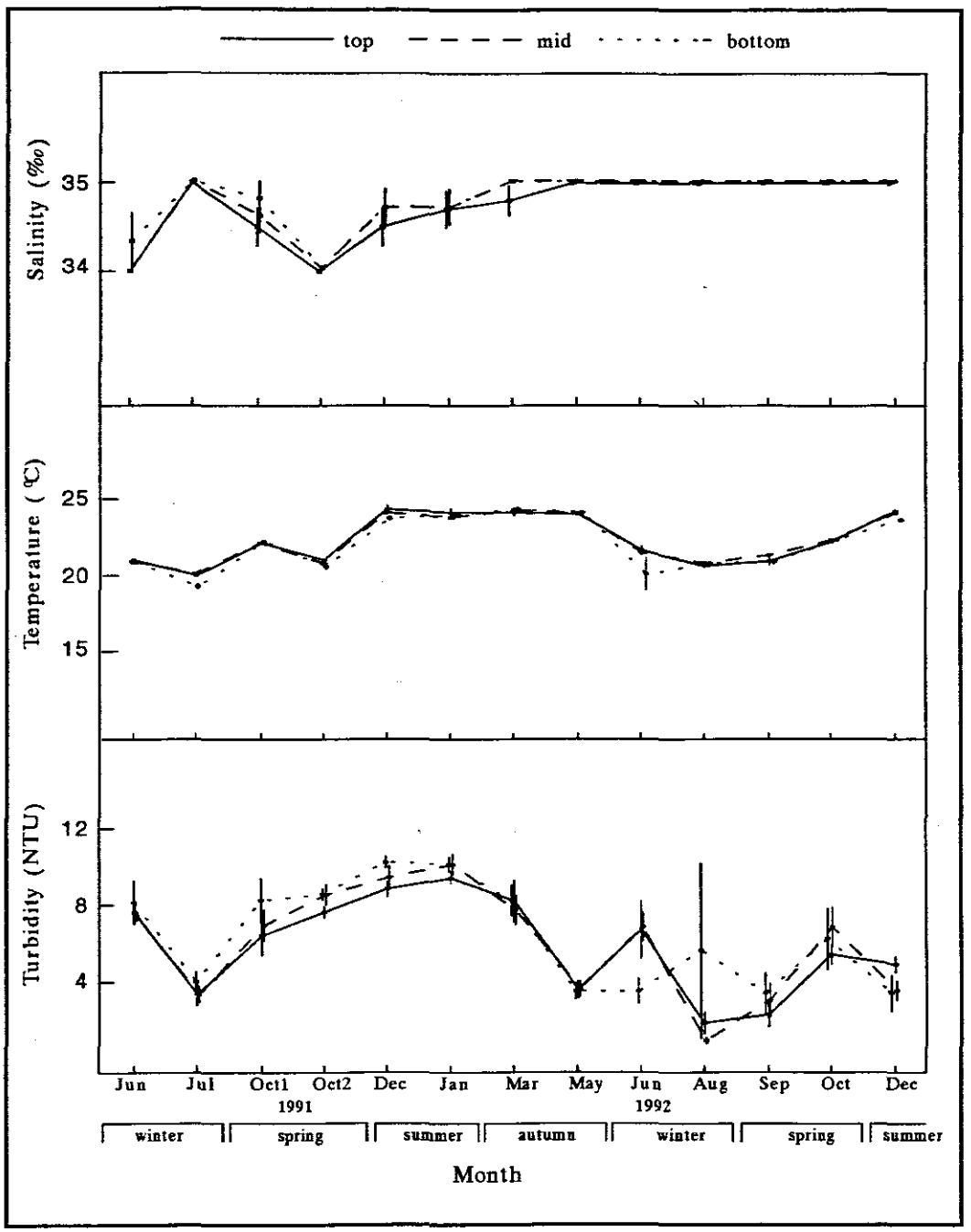


Figure 4.1. Mean monthly variations (± 1SE) of the environmental variables (salinity, temperature and turbidity) for top, mid and bottom samples in Durban Harbour for the study period.

4.2.2 Assemblage Composition and Relationships to Environmental Variables

A total of 8 797 fish larvae, representing 64 families and 144 taxa, was collected between June 1991 and December 1992 (Table 4.1 and Appendix II). Clupeidae was the most abundant family comprising 30% of the total catch, followed by Gobiidae (14.8%), Engraulidae (10.2%), Blenniidae (10.1%), Tripterygiidae (8.9%), Sparidae (5.7%), Myctophidae (3.7%) and Haemulidae (3.1%) (Figure 4.2). Other families contributing more than 1% were Sciaenidae (1.9%), Soleidae (1.5%) and Leiognathidae (1.0%).

The most abundant species was the blueline herring, *Herklotsichthys quadrimaculatus*, which accounted for 29.7% of the total catch. In order of abundance, the following species were also relatively abundant: *Stolephorus holodon* (9.8%), Blenniid 1 (9.3%), Tripterygiid 1 (8.8%), Gobiid 12 (6.7%), Gobiid 27 (6.3%) and *Rhabdosargus sarba* (4.5%). The larvae of *Pomadasys commersonnii*, *S.bleekeri*, *Argyrosomus* sp. and *Scopelopsis multipunctatus* each contributed between 1.0 and 4.0 % of the total (Table 4.1).

Multiple regression analysis for fish larvae in each estuarine-association group showed that different combinations of environmental variables accounted for some of the variation in larval densities and which was species-specific (Table 4.2). With all taxa in the regression model, 22% of the variation in larval densities was accounted for by salinity, turbidity and temperature with densities being higher at higher salinities and lower turbidities and temperatures. Temperature and salinity accounted for 31% of the variation in larval densities of estuarine-dependent taxa where densities were higher at lower temperatures and higher salinities ($P < 0.001$). Larval densities of the sparid *R.sarba,* an estuarine-dependent species, were significantly correlated to salinity, temperature and turbidity ($R = 0.65$; $P < 0.001$). In contrast, larval densities of the haemulid *P.commersonnii*, also an estuarine-dependent species, were only correlated to temperature ($R = 0.30$; $P < 0.001$). For taxa partially dependent on estuaries, no significant correlations were detected between environmental variables and larval densities, except for *S.bleekeri* where temperature was the most significant variable ($P < 0.001$). Density variations of taxa not dependent on estuaries were explained by all three environmental variables in varying degrees (4 to 23% of the model, Table 4.2).

Table 4.1. Total catch, body length and developmental stage for all fish larvae collected in Durban Harbour. (Le, leptocephali; Ys, yolk sac; Pr, preflexion; Fl, flexionJu, juvenile; F, flood tide; E, ebb tide - *abundant;very abundant)**

Family	Species	Rank overall	Total catch no.	Total catch (mean no.100m^{-3})	%	Body length (mm) mean	Body length (mm) range	Developmental stages	Presence	Ju & Ad present[A]
ESTUARINE-DEPENDENT										
Estuarine residents										
Gobiidae	*Omobranchus woodi*		20	0.11	0.3	5.4	2.5-12.0	Pr,Fl,Po	F,E	
	Redigobius sp.		5	0.02	0.1	5.2	3.0-7.0	Pr, Po	F,E	
	Psammogobius knysnaensis		1	<0.01	<0.1	6		Po	E	
Eleotridae	Eleotrid 4		2	0.01	<0.1	13		Po	F,E	
Marine spawners dependent on estuaries										
Elopidae	*Elops machnata*		28	0.10	0.3	32.4	28.0-35.0	Le	F,E	+
Engraulidae	*Thryssa vitrirostris*		38	0.18	0.5	7.7	5.0-13.0	Pr,Fl	F,E	+
Teraponidae	*Terapon jarbua*		13	0.06	0.1	3.9	3.0-5.5	Pr,Fl	F,E	+
Haemulidae	*Pomadasys commersonnii*	8	238	1.02	2.7	5.9	3.0-13.0	Pr,Fl,Po	F*,E	+
Sparidae	*Acanthopagrus berda*		29	0.11	0.3	9	5.0-11.0	Fl,Po	F*,E	+
	Rhabdosargus holubi		5	0.02	0.1	9.9	7.5-11.0	Po	F	+
	Rhabdosargus sarba	7	411	1.72	4.5	4.9	2.5-13.5	Pr,Fl,Po	F,E*	+
Monodactylidae	*Monodactylus argenteus*		13	0.06	0.2	4.7	3.0-6.5	Pr,Fl,Po	F,E	+
PARTIALLY ESTUARINE-DEPENDENT										
Estuarine and marine spawners										
Syngnathidae	*Hippichthys heptagonus*		2	0.01	<0.1	24	23.0-25.0	Po	E	+
Ambassidae	*Ambassis* sp.	14	64	0.34	0.9	3.5	2.0-5.5	Pr,Fl,Po	F,E	+
Gobiidae	*Croilia mossambica*	13	95	0.34	0.9	11.2	8.5-12.5	Po	F*,E	
	Taenioides esquivel		3	0.02	0.1	8	4.0-10.5	Pr,Po	F,E	
Marine spawners with juveniles abundant in estuaries										
Sciaenidae	*Argyrosomus sp.*	*10*	*107*	*0.46*	*1.2*	*5.5*	*2.5-11.0*	*Pr,Fl,Po*	*F*,E*	+
Mugilidae	Mugilid spp.	18	54	0.21	0.6	4	2.0-10.0	Pr,Fl,Po	F,E	+
Soleidae	*Solea bleekeri*	9	131	0.58	1.5	3.8	2.5-7.0	Pr,Fl,Po	F*,E	+

cont.

Table 4.1 cont.

Marine spawners with juveniles at sea and in estuaries										
Clupeidae	*Hilsa kelee*		1	<0.01	<0.1	30		Pr	E	+
Engraulidae	*Stolephorus holodon*	2	775	3.68	9.8	12.2	4.0-27.0	Pr,Fl,Po	F**,E*	+
Hemiramphidae	*Hyporhamphus improvisus*		3	0.01	<0.1	5		Pr	E	+
Platycephalidae	*Platycephalus indicus*		15	0.07	0.2	4.7	2.0-9.0	Pr,Fl,Po	F,E	+
Sillaginidae	*Sillago sihama*		5	0.02	<0.1	11.2	8.0-15.0	Po	F,E	+
Sciaenidae	*Johnius dussumeiri*		10	0.04	0.1	4.6	3.0-6.0	Pr,Fl,Po	F	+
Leiognathidae	*Leiognathus equula*		28	0.15	0.4	4.6	2.0-8.5	Pr,Fl,Po	F,E	+
Sphyraenidae	*Sphyraena jello*		1	<0.01	<0.1	3.5		Pr	E	+
ESTUARINE-INDEPENDENT[B]										
Reef and shore taxa										
Clupeidae	*Herklotsichthys quadrimaculatus*	1	2748	11.19	29.7	7.7	3.8-24.0	Ys,Pr,Fl,Po	F**,E**	
Bregmacerotidae	*Bregmaceros atlanticus*	19	50	0.21	0.5	5	3.0-12.0	Pr,Fl,Po	F*,E	
Gobiesocidae	*Lepadichthys* sp.1		31	0.14	0.4	4.5	1.5-6.8	Pr,Fl,Po	F,E	
Notocheiridae	*Iso natalensis*		22	0.10	0.3	9.2	4.5-15.0	Pr,Fl,Po	F*,E	
Haemulidae	*Pomadasys olivaceum*		27	0.10	0.3	11.5	7.0-22.0	Po	F,E	+
Sparidae	*Pagellus bellottii natalensis*		24	0.10	0.3	4.3	3.0-8.0	Pr,Fl,Po	F,E	
	Sparid 6		49	0.17	0.5	5.9	3.0-11.0	Pr,Fl,Po	F,E	
Nemipteridae	*Nemipterus* sp.	17	58	0.24	0.6	3	2.0-6.0	Pr,Fl	F,E*	
Sciaenidae	*Umbrina ronchus*	19	45	0.21	0.5	4.4	2.5-11.0	Pr,Fl,Po	F,E	
Leiognathidae	*Secutor insiduator*	16	45	0.24	0.6	4.4	2.5-11.0	Pr,Fl,Po	F,E	
Carangidae	*Decapterus* sp.2		25	0.13	0.3	3.6	2.0-5.0	Pr,Fl	F*,E	
Blenniidae	Blenniid 1	3	797	3.50	9.3	4.5	2.5-16.0	Pr,Fl,Po	F*,E*	
	Blenniid 6		34	0.14	0.4	6.7	4.0-18.0	Pr,Fl,Po,Ju	F,E	
Tripterygiidae	Tripterygiid 1	4	768	3.32	8.8	5.9	3.0-15.0	Pr,Fl,Po	F*,E**	
Callionymidae	*Draculo celatus*	19	48	0.21	0.5	3.7	2.0-10.0	Pr,Fl,Po	F,E	
Gobiidae	Gobiid 12	5	638	2.54	6.7	5.6	2.5-11.0	Pr,Fl,Po	F*,E*	
	Gobiid 27	6	506	2.38	6.3	5.5	2.0-14.0	Pr,Fl,Po	F*,E**	
Scombridae	Scombrid 4		16	0.10	0.3	3.6	2.5-5.0	Pr	F,E	
Tetraodontidae	*Arothron immaculatus*	12	92	0.35	0.9	3.3	1.5-8.0	Pr,Fl,Po	F,E*	+
Cynoglossidae	*Cynoglossus* sp.1	20	42	0.19	0.5	6.4	2.0-12.0	Pr,Fl,Po	F,E	

cont.

Table 4.1 cont.

	Oceanic taxa								
Photichthyidae	*Vinciguerria attenuatta*		32	0.14	0.4	9.8	5.8-16.0	Fl,Po	F*,E
Gonostomatidae	*Cyclothone pseudopallida*		37	0.18	0.5	8.3	5.0-12.0	Fl,Po	F*,E
Myctophidae	*Diaphus* sp.2	19	47	0.21	0.5	5.6	3.0-10.0	Pr,Fl,Po	F*,E
	Hygophum proximum		33	0.16	0.4	5.5	3.4-8.0	Pr,Fl,Po	F*,E
	Lamapanyctus alatus	15	59	0.25	0.7	4.8	2.8-7.5	Pr,Fl,Po	F*,E
	Scopelopsis multipunctatus	11	96	0.43	1.1	4.8	3.0-7.0	Pr,Fl,Po	F*,E*

Total number of larvae = 8797
Total number of taxa = 144
Total number of families = 64

[A]Wallace 1975a; Hay *et al.* (1993); Beckley *et al.* (1994); Guastella (1994)
[B]*Taxa contributing <0.3% of the total catch are listed in Appendix II*

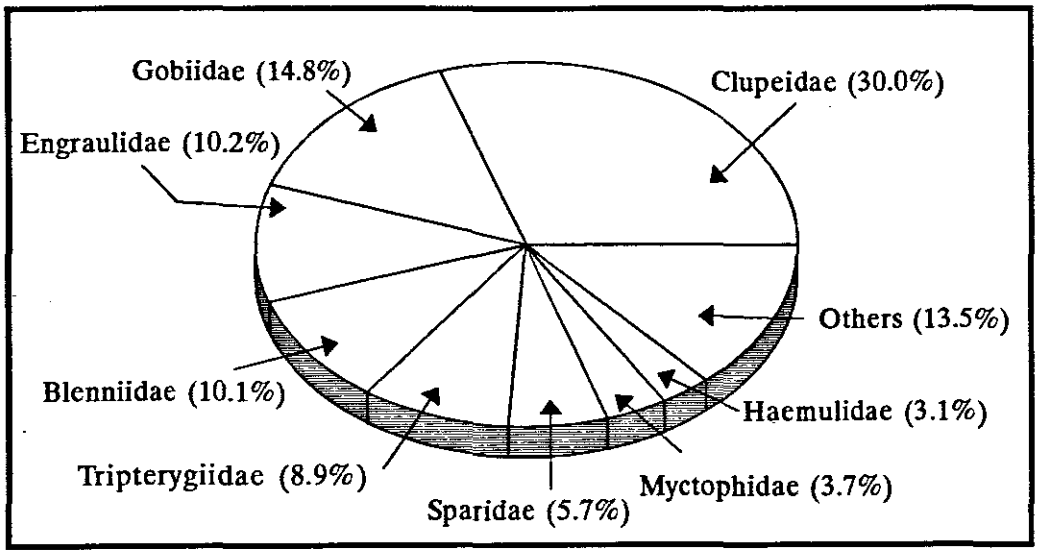


Figure 4.2. Percentage contribution of dominant families for all taxa collected in the study.

Table 4.2. Stepwise regression statistics of larval fish densities versus environmental variables (sa, salinity; te, temperature; tu, turbidity) for each estuarine-association group and the most abundant species in each group, in Durban Harbour. (adj; adjusted R^2; coefficient of determination; R, correlation coefficient; F, F statistic; — , adjusted $R^2 = 0$)

Estuarine-association group	adjR^2	R	F	significant variables
All taxa	0.22	0.47	21.91***	sa***; -tu***; -te**
Estuarine-dependent	0.31	0.56	50.96***	-te***; sa***
Rhabdosargus sarba	0.42	0.65	55.80***	-te***; sa***; -tu*
Pomadasys commersonnii	0.09	0.30	24.37***	-te***
Partially estuarine-dependent	–	–	–	–
Croilia mossambica	–	–	–	–
Solea bleekeri	0.14	0.37	19.29***	-te***; tu*
Arygyrosomus sp.	–	–	–	–
Stolephorus holodon	–	–	–	–
Estuarine-independent	0.22	0.47	22.58***	sa***; -tu***; -te*
Herklotsichthys quadrimaculatus	0.22	0.47	22.52***	-te***; sa***; -tu**
Tripterygiid 1	0.04	0.20	10.88**	-tu**
Blenniid 1	0.23	0.48	24.23***	sa***; -tu***; -te**
Gobiid 12	0.08	0.28	10.75***	-te***; sa*
Scopelopsis multipunctatus	0.15	0.39	21.09***	-te***; -tu*

P<0.05; **P<0.01;***P<0.001

4.2.3 Estuarine-Association

Larvae of species which are marine spawners and are not dependent on estuaries (categories IIIa, IIIb) dominated the total catch, both in terms of density of larvae (78.0%) and the number of taxa (80.6%) (Figure 4.3). A total of 28 taxa, which are dependent on estuaries to some degree (categories I and II), was recorded and contributed to 22.0% of the total density. Thirteen of the 28 taxa are totally dependent on estuaries at some stage in their life cycle (categories Ia and IIa) but were not particularly abundant (2.2% of total catch). No larvae of catadromous or euryhaline freshwater species were collected in this study.

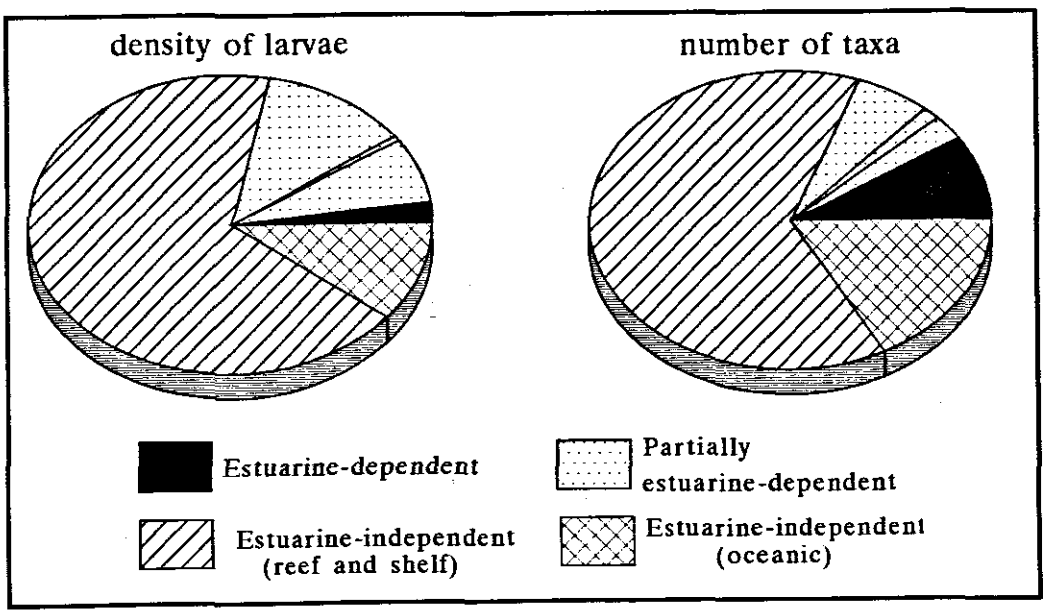


Figure 4.3. Percentage contribution of the estuarine-association categories, in terms of density of larvae and number of taxa, for all taxa sampled in the study.

4.2.4. Temporal and Spatial Trends in Larval Fish Density

Densities of all taxa as a whole peaked in August 1992 (118 larvae per $100m^3$) and was lowest in early October 1991 (2 larvae per $100m^3$, Figure 4.4A). The highest mean density of estuarine-dependent taxa occurred in June 1992 (18 larvae per $100m^3$) and the lowest in early October 1991 (0.2 larvae per $100m^3$, Figure 4.4B). The peak in June 1992 was due to an abundance of larval *R.sarba* and *P.commersonnii* with a smaller peak in July 1991 (14 larvae per $100m^3$) being due to only *R.sarba* (Figure 4.5). Peaks in densities of partially estuarine-dependent taxa occurred in late October 1991 and December 1992, reaching a maximum of 20 larvae per $100m^3$ (Figure 4.4C). These peaks in abundance were due to the presence of *S.holodon* (Figure 4.5). Estuarine-independent taxa were most abundant in August 1991 (109 larvae per $100m^3$) and least abundant in early October 1991 (2 larvae per $100m^3$) (Figure 4.4D). The peak in abundance in August 1992 was mainly due to *H.quadrimaculatus* but also three other abundant reef-associated species (Figure 4.5).

Three-way ANOVAs showed that larval densities of all taxa and each estuarine-association group did not differ significantly between ebb and flood tides ($P > 0.05$), although, individual species did (Table 4.3). All of the abundant estuarine-associated species, except *R.sarba*, had significantly higher densities on flood tides. Conversely, only two of the independent taxa, Tripterygiid 1 and Gobiid 12, had significantly different densities with tide which were higher on ebb tides ($P < 0.05$). Depth was a significant factor for all groups and individual species in each group, except for two species in the independent group, with densities being highest in bottom samples (Table 4.3). Densities of Gobiid 12 were generally higher in bottom and mid water samples, although it was not significant ($P = 0.07$). Note that the only abundant species which showed no trends with depth was a myctophid species, *Scopelopsis multipunctatus*, an oceanic-associated species. Although month was a significant effect for all groups and individual species, the mean squares were relatively small (Table 4.3). The tide x depth interaction was significant at $P < 0.01$ for only *S.bleekeri* and at $P < 0.05$ for *Argyrosomus* sp. and *S.holodon,* which are all partially estuarine-dependent. The tide x month and depth x month interactions were significant for particularly for *S.bleekeri* and *H.quadrimaculatus* ($P < 0.001$).

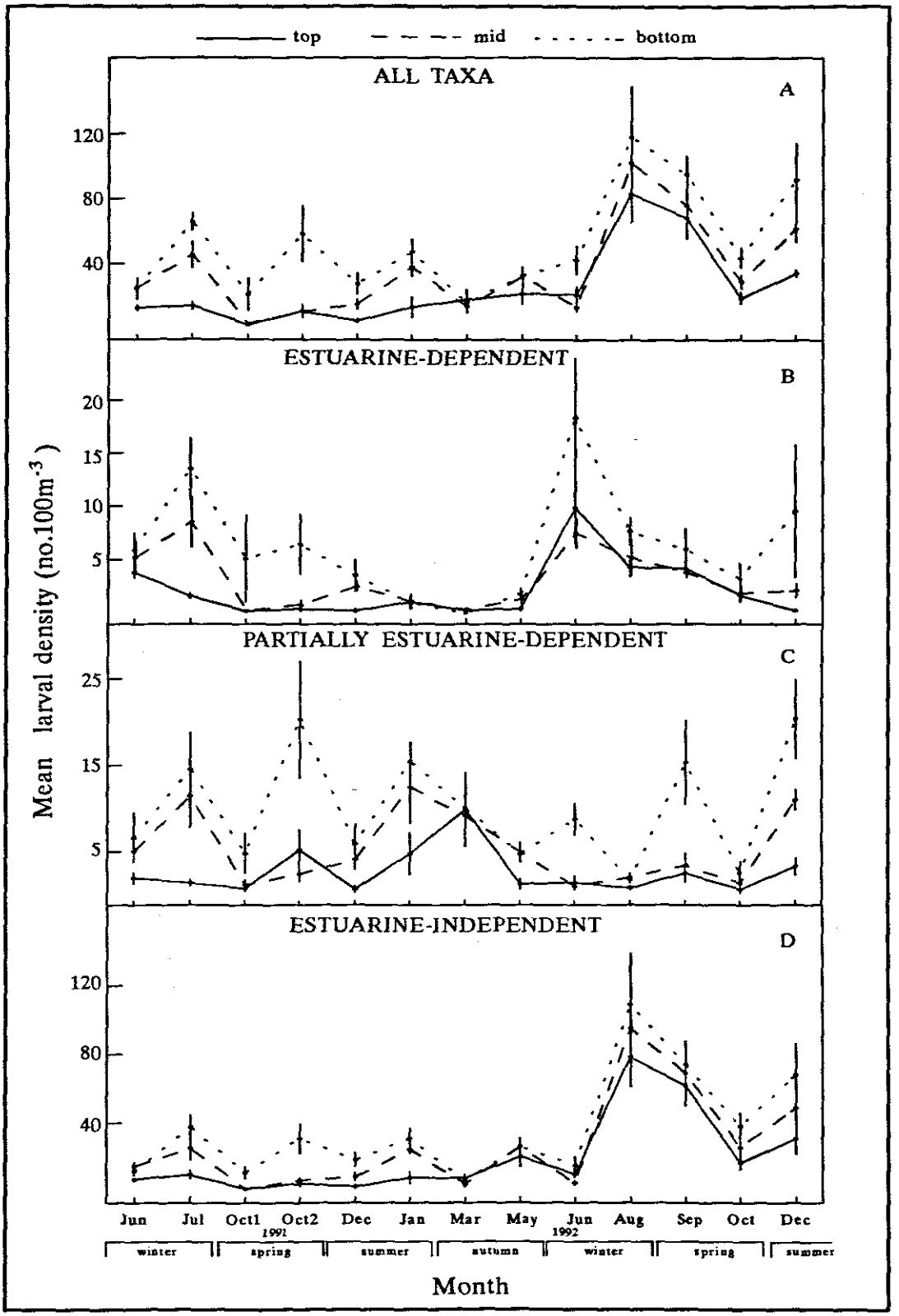


Figure 4.4. Mean monthly variations in larval densities (± 1SE) in top, mid and bottom samples for all taxa together (A), estuarine-dependent taxa (B), partially estuarine-dependent taxa (C) and estuarine-independent taxa (D).

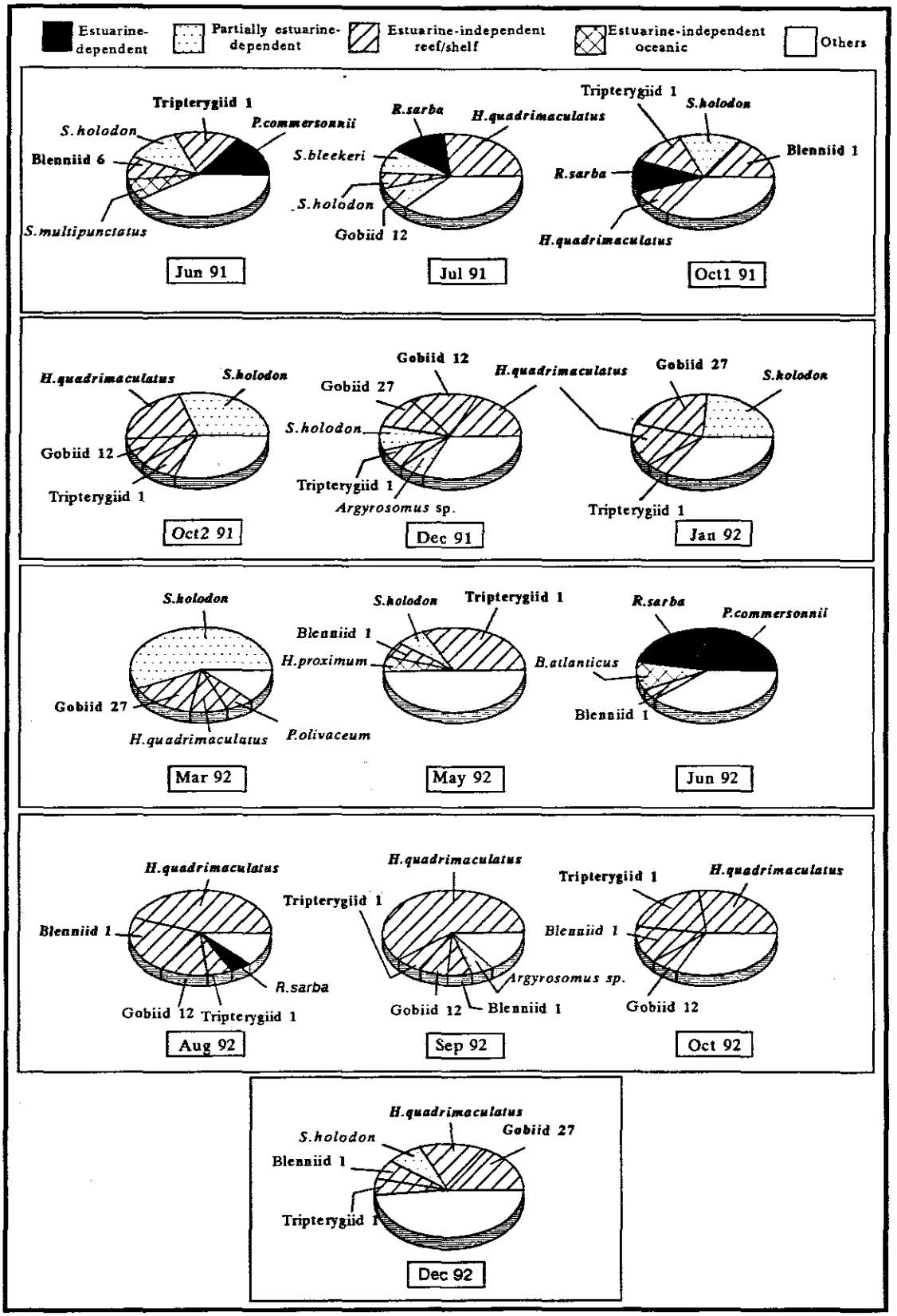


Figure 4.5. Percentage contribution of the most abundant species in the total catch sampled each month in Durban Harbour.

Table 4.3. Mean squares and significance levels for three-way ANOVA of densities of the most abundant species in each estuarine-association group, in Durban Harbour. (DF = degrees of freedom)

Estuarine-association group	Main effects			2-way interactions		
	Tide (F/E)[A] (DF=1)	Depth (T,M,B)[B] (DF=2)	Month (1 to 12)[C] (DF=11)	Tide x Depth (DF=2)	Tide x Month (DF=11)	Depth x Month (DF=22)
All taxa	0.1	2.87***(B>M>T)	2.06***	0.10	0.21*	0.19**
Estuarine-dependent	0.19	1.45***(B>M>T)	1.32***	0.06	0.15*	0.13*
Rhabdosargus sarba	0.25*(E>F)	0.45***(B>MT)	1.33***	0.002	0.08	0.09*
Pomadasys commersonnii	1.19***(F>E)	0.20***(B>MT)	0.65***	0.05	0.18***	0.04
Partially estuarine-dependent	1.91***(F>E)	4.11***(B>M>T)	0.84***	0.49*	0.22*	0.19*
Croilia mossambica	0.28**(F>E)	0.32***(B>M>T)	0.10***	0.07	0.03	0.05*
Solea bleekeri	0.47***(F>E)	0.22***(BM>T)	0.37***	0.13**	0.07***	0.07***
Arygyrosomus sp.	0.62***(F>E)	0.32***(B>MT)	0.13***	0.08*	0.09***	0.04
Stolephorus holodon	0.52*(F>E)	1.73***(BM>T)	0.95***	0.47*	0.18	0.14
Estuarine-independent	0.08	2.24***(B>M>T)	2.93***	0.11	0.29**	0.22*
Herklotsichthys quadrimaculatus	0.01	1.70***(B>M>T)	5.0***	0.26	0.21*	0.23***
Tripterygiid 1	0.42*(E>F)	0.84***(B>M>T)	1.28***	0.16	0.42***	0.09
Blenniid 1	0.22	0.55***(B>MT)	2.07***	0.12	0.33***	0.07
Gobiid 12	0.53*(E>F)	0.25	1.05***	0.09	0.10	0.13
Scopelopsis multipunctatus	0.04	0.01	0.39***	0.06	0.04	0.01

*p<0.05;**p<0.01;***p<0.001

[A] tide where densities are significantly higher is indicated in parentheses. F, flood tide; E, ebb tide

[B] depths where densities are highest are indicated in parentheses and Fig.4.4 (Groups only). T, top; M, mid; B, bottom

[C] months where densities are highest are indicated in Fig. 4.4 (Groups only)

4.2.5 Developmental Stages

Developmental stages of larvae in the estuarine-dependent group were predominantly young larvae (65.0% of the total) but with 30.2% of the larvae at postflexion stages (Figure 4.6). The leptocephalus larvae, from the estuarine-dependent group, were those of *Elops machnata* (ladyfish). Marine spawners partially estuarine-dependant were present in all developmental stages but mainly as postflexion larvae (55.5%). Marine stragglers, which are not dependent on estuaries, were predominantly preflexion and flexion larvae (72.5%). The yolk sac stages were *H.quadrimaculatus,* the juvenile stages Blennid 6, *Caranx sexfaciatus,* Melanostomiid 1 and *Schindleria praematura,* and the adult stage *S.praematura* (Table 4.2). The leptocephali in this category were eel species.

The proportions of developmental stages changed in each month sampled with young larvae (preflexion and flexion) being most abundant in late October 1991 and from August to December 1992. i.e. late winter, spring and early summer months (Figure 4.7). Postflexion larvae were most abundant in December 1991 and particularly in March 1992. The leptocephali occurred in summer (December 1991 and January 1992), the adult *S.praematura* in late October 1991, and the yolk sac stages of *H.quadrimaculatus* in August 1992.

All developmental stages of the sparid *R.sarba* were collected on both tides and at all depths but the larvae were more abundant on ebb tides and in mid and bottom waters (Figure 4.8). More preflexion larvae of the haemulid *P.commersonnii* were present on flood tides with less larvae on ebb tides which were mainly flexion and postflexion. Larvae of all developmental stages of the sciaenid *Argyrosomus* sp. were far more abundant on flood tides, and in bottom waters for both flood and ebb tides - only preflexion stages were collected in the top samples of the ebb tide. *S.holodon* showed a similar trend to *Argyrosomus* sp., but with fewer larvae on flood tides. Larvae of the estuarine-independent species, *H.quadrimaculatus* and Blenniid 1, were predominantly preflexion on both flood and ebb tides and at all three depths sampled (Figure 4.8).

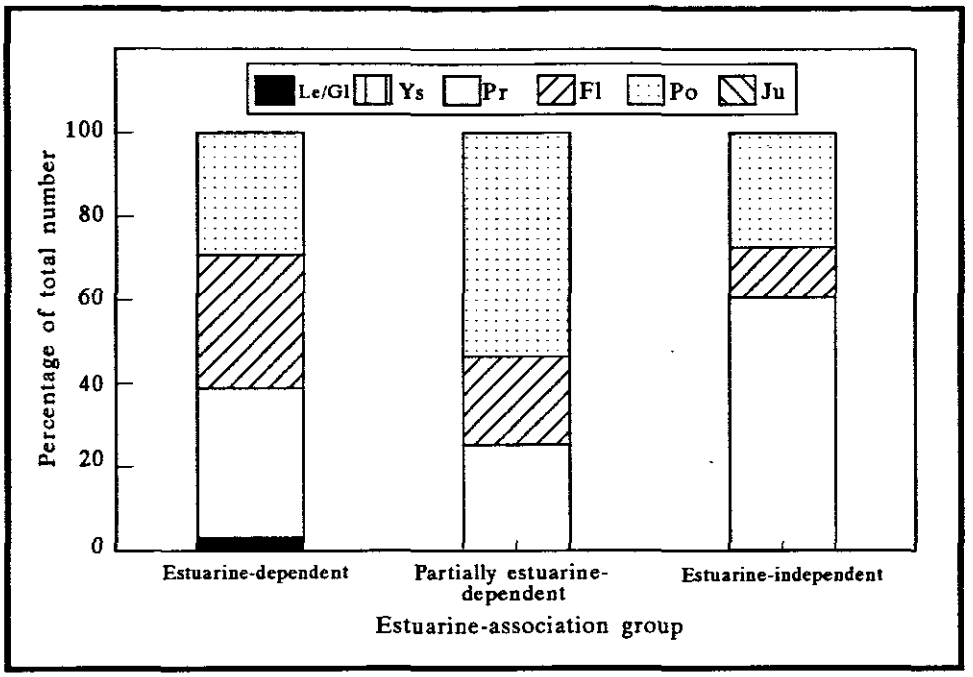


Figure 4.6. Percentage composition of the different developmental stages of all larvae for each estuarine-association category. Gl, glass eel; Le, leptocephali; Ys, yolk sac; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile.

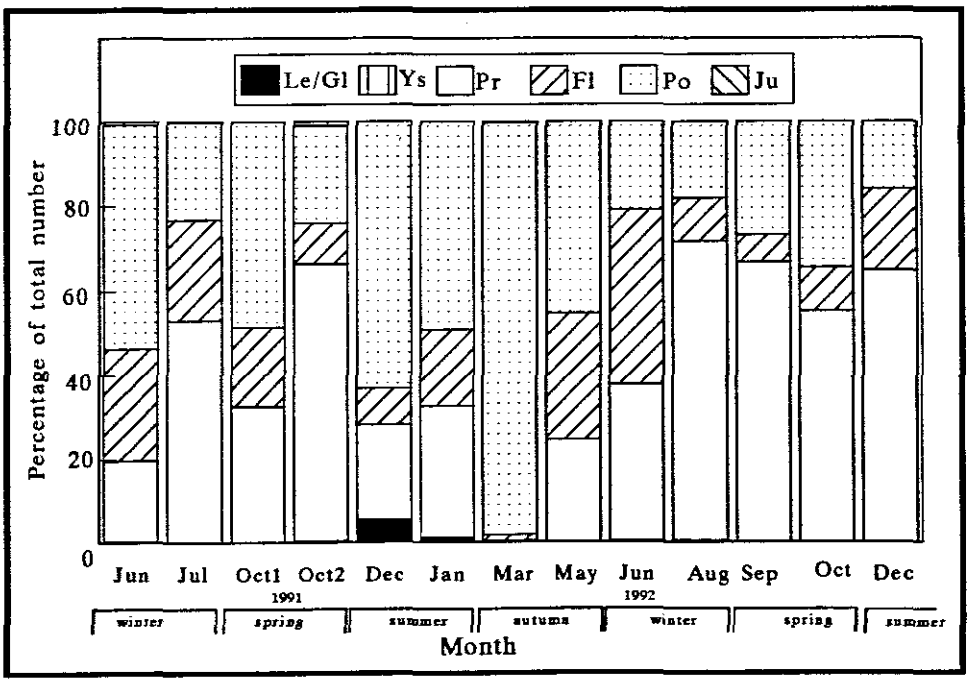


Figure 4.7. Monthly percentage composition of developmental stages of all larvae sampled in the study. Gl, glass eel; Le, leptocephali; Ys, yolk sac; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile.

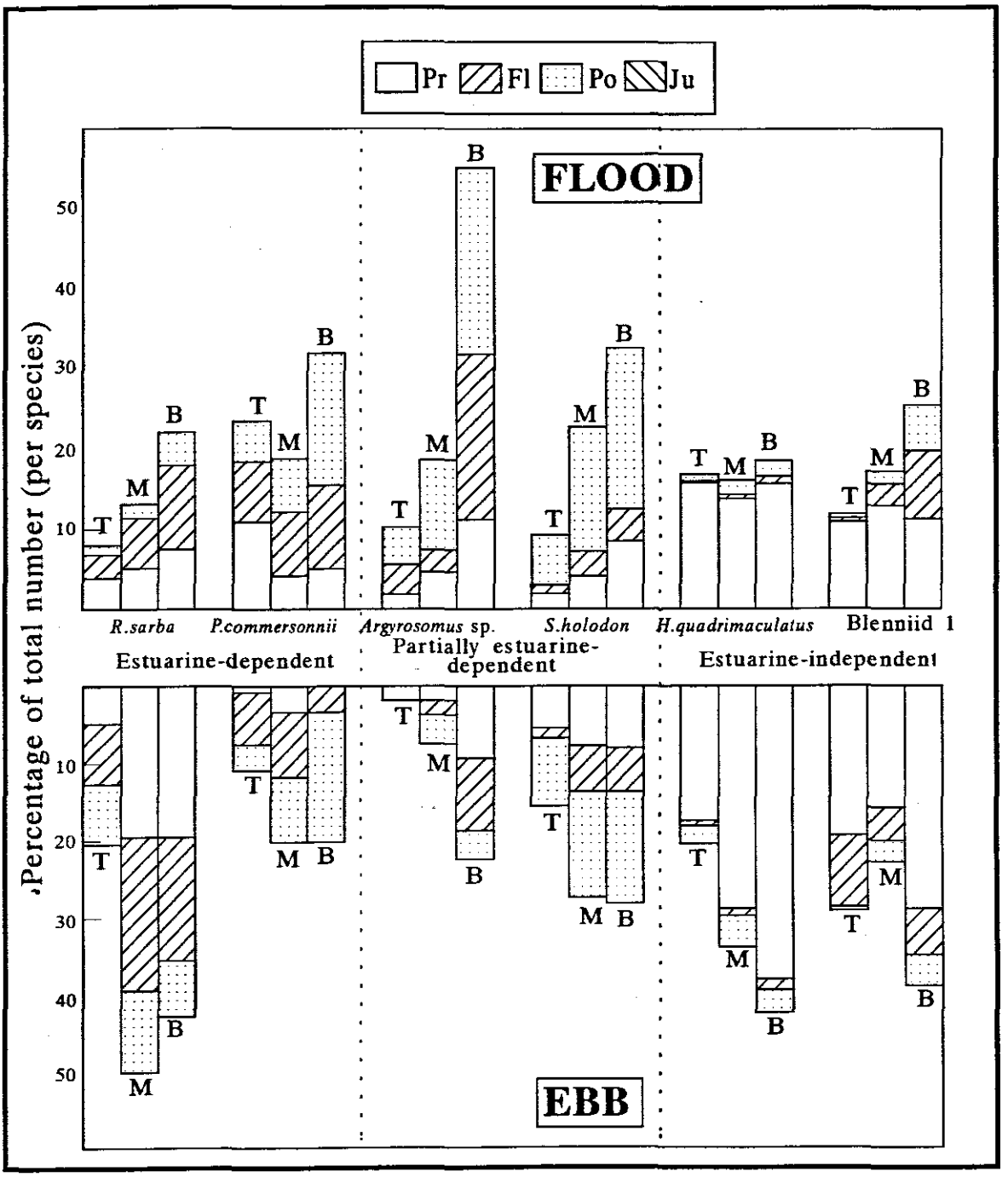


Figure 4.8. Percentage composition of developmental stages for the most abundant species in each estuarine-association category, on flood and ebb tides for the study period. (T, top; M, mid; B, bottom)

4.3. Discussion

4.3.1. Composition of the Larval Fish Assemblage

Biological surveys during the 1950s showed that Durban Harbour supported a very diverse fauna, with 186 fish species being recorded (Day and Morgans 1956). Many of the marine fish species recorded in the bay are euryhaline estuarine species typical of other estuaries in KwaZulu-Natal (Wallace 1975a). Recent fish surveys in the harbour have shown that the fish life is still abundant but with fewer species (Hay *et al.* 1993; Beckley *et al.* 1994; Cyrus and Forbes 1994; Graham 1994; Guastella 1994). Species which are particularly abundant in the system as juveniles and/or adults are *P.commersonnii, A.berda, R.sarba, Argyrosomus hololepidotus, Leiognathus equula, Gerres filamentosus, Hilsa kelee* and mullet species. Wallace (1975a) suggested that the fish assemblage in Durban Harbour is merely an extension of the marine inshore population since the species composition was representative of the nearshore community. The recent fish surveys, confirm this, since a large proportion of the catch consisted of marine species. This is also reflected in the composition of the larval fish assemblage of the present study, where 81% (116 taxa) of all taxa collected and 78% of total abundance were marine stragglers. Compared with the juvenile and adult fish assemblage in previous studies (Hay *et al.* 1993; Beckley *et al.* 1994; Cyrus and Forbes 1994; Graham 1994; Guastella 1994), larvae of different species dominated the catch (*H.qaudrimaculatus*, *S.holodon* and Blenniid 1), with larvae of *P.commersonnii*, *A.berda, Argyrosomus* sp. (*hololepidotus* ?) and *L.equula* being relatively abundant (Table 4.2). Mugilids are one of the most abundant fish species in KwaZulu-Natal estuaries (Wallace 1975a; Whitfield 1994a), particularly the juveniles. Larvae of mugilids were relatively abundant in Durban Harbour (ranked 18th overall), however, there was a paucity of mullet larvae in other large estuaries in KwaZulu-Natal, such as the St Lucia Estuary (see Table 6.1, Chapter 6) and Richards Bay Harbour (see Table 5.1, Chapter 5). Mugilid larvae were also abundant in the surf zone adjacent to the St Lucia Estuary mouth (see Table 8.1, Chapter 8). This suggests that, in KwaZulu-Natal, mullet species enter the estuarine habitat at a larger size range than larval stages, since larval stages were more prevalent in marine conditions.

Begg (1978) listed four main impacts of the harbour development on Durban Bay: (1) elimination of marginal vegetation (2) removal of suitable substrates as feeding grounds (3) industrial pollution and (4) increased tidal exchange. The increased tidal exchange would most influence the composition of the ichthyoplankton in the harbour and explains the dominance of marine straggler larvae in the present study. Studies on the bays and estuaries of California indicated that the size of the opening of an embayment to the sea was the best predictor of the number of species in the embayment (Horn and Allen 1976). The amount of water entering Durban Harbour over a spring flood tide was estimated to be 13.5 x 10^6 m^3 (Forbes *et. al.* 1994) with the majority of the taxa, in the present study, being marine stragglers. Richards Bay Harbour (190 km north of Durban Harbour) has a larger tidal volume (25 x 10^6 m^3) with 72% of all taxa being marine stragglers (Figure 5.3). St Lucia Estuary, on the other hand, has only 2 x 10^6 m^3 entering the system with 44% of the taxa being larvae of marine stragglers (see Figure 6.3, Chapter 6). Whangateau Harbour, in northern New Zealand, is a small (9.2 km^2), bar-built estuary with extensive tidal flushing and therefore essentially marine conditions (Roper 1986). The composition of fish larvae in Whangateau Harbour was similar to adjacent nearshore marine environment. In contrast, Neira and Potter (1992) found a paucity of marine-spawned larvae in the Wilson Inlet (south-western Australia) which was attributed to the restricted tidal exchange that occurs through the narrow and shallow entrance channel of that system.

Are the dominant marine species in Durban Harbour recruiting into the bay at the larval stage ?. The studies by Wallace (1975a,b) and Wallace and van der Elst (1975) suggested that active recruitment of juveniles into KwaZulu-Natal estuaries is quantitatively more important than recruitment of larval stages but they did not sample larval stages adequately. Of the 144 larval taxa collected during the present study, 27 have been recorded also as juveniles and/or adults in Durban Harbour (Table 4.1 - last column). Twenty-one of the 27 species (78%) are fish species which are dependent or partially dependent on estuaries and were collected at larval stages of development in the present study. e.g. *R.sarba* and *P.commersonnii.* This suggests that the estuarine-associated fish species utilising Durban Harbour as a nursery area are recruiting into the system as larvae. However, since the harbour mouth is dredged and thus deep, the majority of marine straggler larvae (Appendix II) entering the system on flood tides (in

pulses of marine water) may not survive at all or else get washed out to sea again on the outgoing tide. There is evidence of inshore spawning by *P.commersonnii* and *R.sarba* (Wallace 1975b) which explains the abundance of larval stages of these species within Durban Harbour. Similarly in Richards Bay Harbour and the St Lucia Estuary, a high percentage (84% and 92%, respectively) of the estuarine-associated fish species recorded as juveniles and/or adults in the systems were also recorded as larvae (see Table's 5.2 and 6.2, Chapters 5 and 6). By comparison, in estuaries of south-western Australia, there is an absence of larvae of most of the marine estuarine-opportunists (equivalent to partially estuarine-dependent taxa in my study) abundant as juveniles and/or adults in the system (Neira and Potter 1992; Neira and Potter 1994) implying that these fish are recruited into these estuaries (Nornalup-Walpole Estuary and Wilson Inlet) as juveniles or adults, rather than larvae.

4.3.2 Larval Fish Abundance in Relation to Environmental Factors

Day and Morgans (1956) found that the salinity, temperature and turbidity of the water in the bay were effectively uniform. The most recent studies have shown that these conditions still prevail: salinities are high (> 30 ‰), temperatures vary seasonally (18 - 27°C) and turbidities are usually low (1 - 22 NTU) (Hay et al. 1993; Beckley *et al.* 1994; Graham 1994; and this study). These marine conditions are therefore suitable for marine and euryhaline estuarine fish species.

Although small ranges in environmental variables were recorded in the present study, larval densities were significantly correlated to temperature, salinity and turbidity which accounted for 22% of the variation in larval densities of all taxa together. Similarly, in Richards Bay Harbour and St Lucia Estuary (Tables 5.2 and 6.2, Chapters 5 an 6) regression analyses suggest that these three environmental variables are important in accounting for the variation of larval densities and is species-specific. In Durban Harbour, peak abundances of larvae of the dominant species occurred during autumn and winter when the water temperatures were lower. Salinity and turbidity have also been shown to be important factors associated with larval and juvenile fish abundances (Cyrus and Blaber 1987a; Whitfield 1994c). Boehlert and Mundy (1988) suggested that it is a

suite of factors associated with tidal flux at particular locations the act as cues for recruiting fish larvae.

4.3.3. Temporal and Spatial Trends in Larval Fish Abundance

Two important recreational and commercial linefish species on the KwaZulu-Natal coast are the kob, *A.hololepidotus* (*Argyrosomus* species A = *A.japonicus* - new taxonomy, Griffiths and Heemstra 1995) and the grunter, *P.commersonnii* (van der Elst 1981). The spawning season for *A.hololepidotus* in the KwaZulu-Natal region is between winter and spring (Griffiths and Hecht 1993) with a subsequent recruitment of the juvenile stage (8 - 15 cm length range) into the estuarine environment (Wallace and van der Elst 1975). *Argyrosomus* sp. (*A.japonicus* ?) larvae were relatively abundant in Durban Harbour during the spring and early summer months (Figure 4.5) in the size range 2.5 - 11.0 mm (mean 5.5 mm, see Table 4.1) which corresponds to the above spawning period and suggests that spawning of this species occurs in close proximity to the harbour mouth. Similarly for *P.commersonnii*, larval stages were abundant in winter months (Figure 4.5) in the size range 3.0 - 13.0 mm (mean 5.9 mm, Table 4.1). This species is known to spawn mainly in winter (Wallace and van der Elst 1975; van der Elst 1981).

Different peaks in larval abundance occurred in Durban Harbour throughout the study period depending on the seasonality of the different species in each estuarine-association group. Fish larvae of estuarine species, in temperate and subtropical estuaries, tend to peak in abundance in spring, summer and early autumn and are least abundant in winter (Melville-Smith and Baird 1980; Whitfield 1989a; Harrison and Whitfield 1990; Tzeng and Wang 1992; Neira and Potter 1994; and see Figures 5.4 and 6.4, Chapters 5 and 6). Peaks in abundance of larval estuarine species in Durban Harbour occurred in similar periods. In the winter months, marine species such as *H.quadrimaculatus,* Blenniid 1 and *B.atlanticus,* comprised a relatively large proportion of the total catch.

Although Durban Harbour is not a typical estuary, the abundance of estuarine-associated fish recorded in the bay suggests that patterns of recruitment and maintenance of those species in the system would be similar to those reported for typical estuarine environments. While some field studies have postulated passive mechanisms of

recruitment, the majority of studies have suggested species-specific behavioural patterns (Boehlert and Mundy 1988; Leis 1991). When fish larvae attain the postflexion developmental stage the caudal fin is formed (Leis and Trnski 1989) and they are, therefore, capable of swimming actively. The stage of development at which fishes are present in inlets or estuaries may, in a large part, determine their ability to behaviourally alter their distribution (Boehlert and Mundy 1988). Recruitment and retention mechanisms into relatively deep estuaries with a two-layered water column, utilise tidal-stream transport (Weinstein *et al.* 1980; Fortier and Leggett 1983; Boehlert and Mundy 1988). In these systems, larval stages of estuarine fishes are often stratified within the water column and many are most abundant near the bottom (Able 1978; Weinstein *et al.* 1980). This two-layered pattern does not exist in some estuarine habitats, such as Whangateau Harbour (8 - 9 m deep), but certain species (for example the goby *Rhombosolea plebia*) do settle on the bottom to avoid being swept out on ebb tides (Roper 1986). The depth of the entrance channel into Durban Harbour is 12.8 m (129 m width) compared with other true estuaries along this coast and so one might expect similar patterns of recruitment and retention mechanisms. The tidal exchange of larvae into and out of Durban Harbour showed definite trends in abundance both with tide and with depth but that it was species-specific. In general, larval densities of estuarine-associated species were higher on flood tides, and in mid and bottom waters suggesting a net input of larvae into the system and an avoidance of the outgoing ebb tides. The trend with depth was most notable for larvae of the sciaenid *Argyrosomus* sp., densities were significantly higher in bottom waters. In estuaries on the east coast of USA, larvae of sciaenids (Atlantic croaker, *Micropogonias undulatus*, and weakfish, *Cynoscion regalis*) have been shown to be more abundant in bottom waters (Hettler and Barker 1993; Rowe and Epifanio 1994). Rowe and Epifanio (1994) found that early stage larvae of weakfish (*Cynoscion regalis*) were significantly more abundant during flood tides in surface waters, and late-stage larvae (> 3 mm) more abundant during flood tides at both surface and mid-depths. A similar pattern was found for *Argyrosomus* sp. larvae in Durban Harbour of the present study, and for *Argyrosomus* sp. in Richards Bay Harbour (Figure 5.8, Chapter 5).

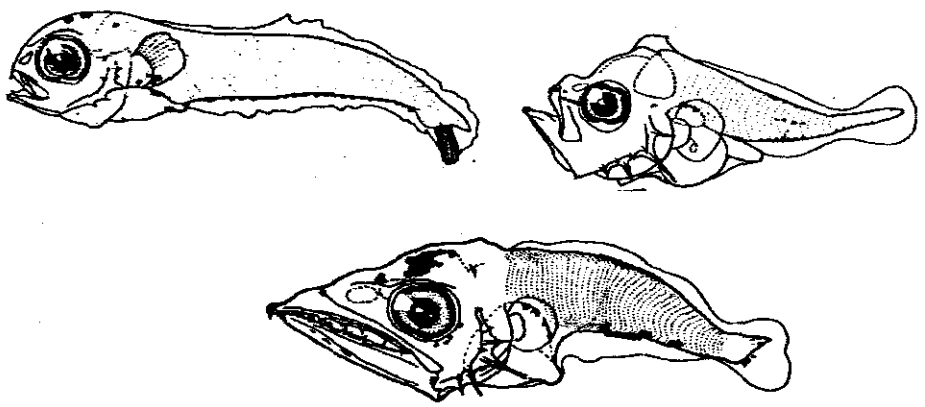
4.3.4 Developmental Stages

It has generally been found that estuarine-associated fish species which spawn in marine waters recruit into estuaries at advanced developmental stages (Melville-Smith and Baird 1980; Melville-Smith 1981; Whitfield 1989a; Harrison and Whitfield 1990; Tzeng and Wang 1992; Neira and Potter 1994) i.e. as old larvae. Conversely, larvae of marine species not dependent on estuaries and which stray into estuarine habitats are predominantly young larvae (preflexion and flexion) (Miskiewicz 1987; Neira *et al.* 1992; Neira and Potter 1994; Harris *et al.* 1995). Similar results were found in the present study (see Figure 4.6) suggesting that estuarine-associated species are either spending some time at sea before entering Durban Harbour or else their spawning grounds are not in close proximity to the bay. Miskiewicz (1986) found that an important factor influencing the length at which larvae of marine species entered the estuarine nursery of Lake Macquarie (Australia) is the proximity of spawning grounds.

The large proportion of young larvae in late winter, spring and early summer of the present study indicated that these months are main spawning periods for certain species. Figure 4.5 suggests that these species are *S.holodon, H.quadrimaculatus*, and Gobiid 27. In the Lower Swan Estuary (south-western Australia), Guaghan *et al.* (1990) similarly found maximum densities of young larvae of certain species during some months providing strong evidence that peak spawning of these species must occur over a similar period.

CHAPTER 5

The Larval Fish Assemblage in Richards Bay Harbour



5. THE LARVAL FISH ASSEMBLAGE IN RICHARDS BAY HARBOUR

5.1. Introduction

Richards Bay Harbour is approximately 190 km north of Durban Harbour on the northern KwaZulu-Natal coast (see Figure 2.1, Chapter 2) and, like Durban Harbour, it also functions as one of the most important shipping ports in southern Africa. In the 15th Century, Portuguese mariners discovered the bay and named it "Rio dos Peixos" meaning "river of many fish " (Anon 1976). This name is an apt description of the bay prior to harbour development since, in those days, it functioned as an important nursery ground for many estuarine-associated fish species with kob (*A.hololepidotus*), spotted grunter (*P.commersonnii*) and seabreams (Sparidae) being plentiful (Millard and Harrison 1954). The bay was renamed as Richards Bay after Sir Richards and his British troops landed there in 1879 (Begg 1978). Richards Bay now consists of a shipping port section in the north and a sanctuary area in the south. The sanctuary area was developed to conserve part of the original system as a nursery area for the fauna which was known to utilise it. With the degradation of other large estuarine systems on the KwaZulu-Natal coast, such as St Lucia Estuary and Durban Bay, the nursery value of Richards Bay has increased.

The earliest ichthyofaunal survey of Richards Bay was undertaken by Millard and Harrison (1954) which was followed by the work of Hemens *et al.* (1970). Post-harbour fish surveys in both the sanctuary and harbour sections were undertaken by van der Elst (1975-1986), Wallace and van der Elst (1975), Hemens *et al.* (1970) and Anon (1978). These studies have shown that the harbour and the sanctuary are still being utilised by many of the estuarine-associated fish species in the region. The significance of Richards Bay as a nusery ground for penaeid prawn postlarvae was established by Forbes *et al.* (1994), who indicated that increasing harbour development could be detrimental to the future prawn stocks. No larval fish studies have been undertaken in either the sanctuary or the harbour in both the pre- and post harbour periods.

The present Chapter describes the composition, abundance and seasonality of larval fishes occurring in Richards Bay Harbour, to establish the role of this habitat in the early life history stages of the fish utilising it. The same questions that were

addressed in Chapter 4, on Durban Harbour, apply to this Chapter (see pg. 29, Chapter 4).

5.2. Results

5.2.1. Environmental Variables

Temporal variations in the environmental variables at the sample site in Richards Bay Harbour (see Figure 2.3, Chapter 2), during the study period June 1991 to November 1992 are shown in Figure 5.1. Water conditions were essentially marine throughout the study period with mean monthly salinity being highest in April 1992 (36.0‰) and lowest in June 1991 (33.5‰). Mean salinity values were significantly higher on ebb tides ($F = 6.67$; $P = 0.01$) but this was only because of a higher mean value of 36.0 ‰ in one of the months sampled (the tide x month interaction was significant, $F = 2.52$ and $P = 0.01$). No significant differences in salinities were detected between the three depths sampled ($F = 1.33$; $P = 0.27$) but mean salinity did differ significantly between sampling dates ($F = 173.27$; $P < 0.0001$).

Seasonal variations in water temperatures were significant ($F = 38.05$; $P < 0.0001$) and reached a maximum of 24.6°C in summer (January 1992) and a minimum of 18.5°C in winter (July 1991, Figure 5.1). Water temperature did not differ significantly between ebb and flood tides ($F = 4.01$; $P = 0.05$) but temperatures were significantly higher in top samples ($F = 4.79$; $P = 0.01$).

Turbidity values differed significantly between sampling dates ($F = 36.04$; $P < 0.0001$) with mean turbidity being highest in March 1992 (33.9 NTU) and lowest in June 1992 (2.1 NTU) (Figure 5.1). Mean turbidities were significantly higher on flood tides ($F = 23.15$; $P < 0.0001$) but did not differ significantly with depth ($F = 0.63$; $P = 0.54$).

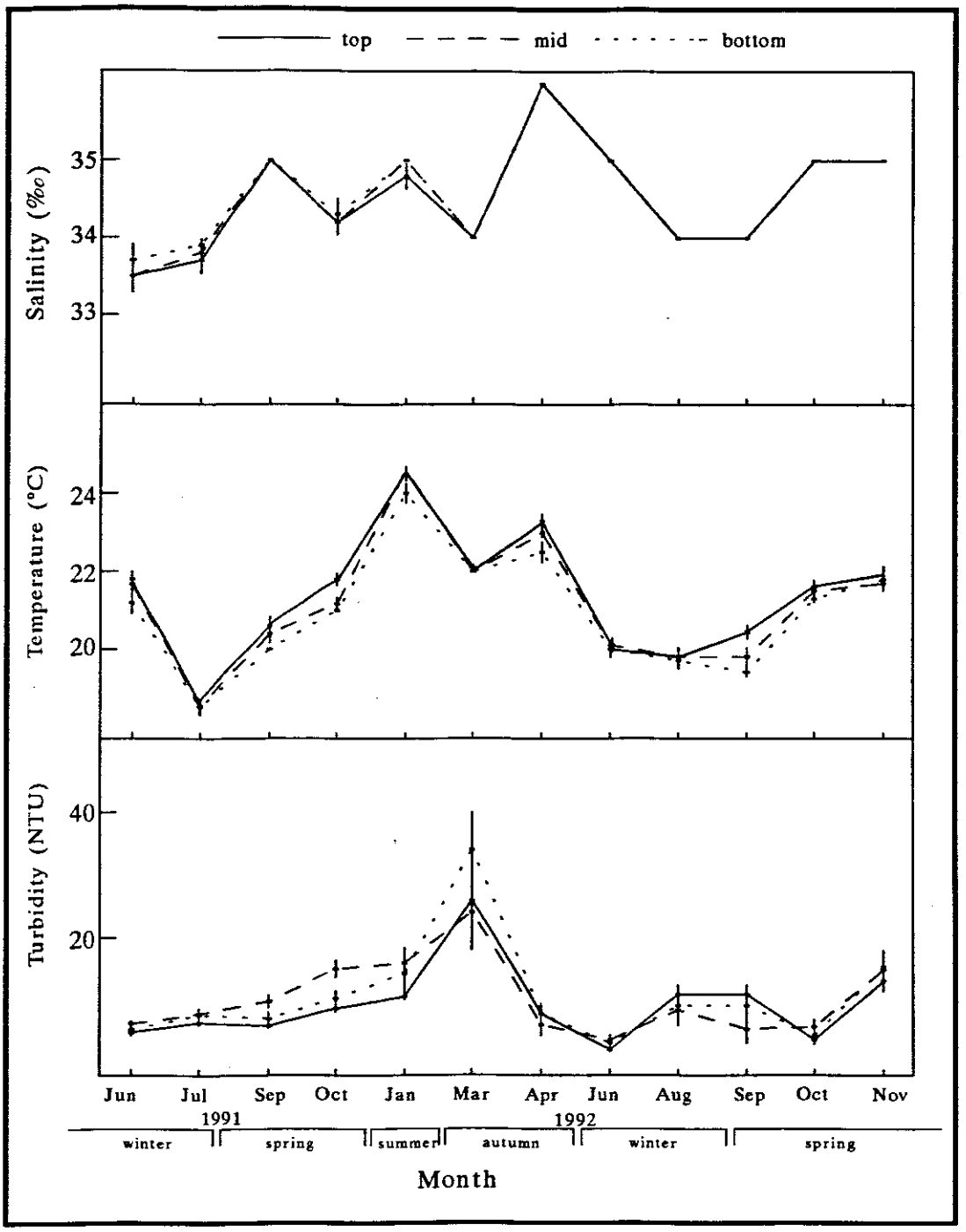


Figure 5.1. Mean monthly variations (± 1SE) of the environmental variables (salinity, temperature and turbidity) for top, mid and bottom samples in Richards Bay Harbour for the study period.

5.2.2. Assemblage Composition and Relationships to Environmental Variables

A total of 7 163 fish larvae, representing 105 taxa and 53 families, was collected throughout the study period in Richards Bay Harbour (Table 5.1). The families Engraulidae and Gobiidae dominated the total catch (50.0% and 36.5%, respectively), followed by Clupeidae (4.2%), Sciaenidae (1.6%), Sparidae (1.4%) and Blenniidae (1.4%) (Figure 5.2). Other families contributing more than 0.5% were Soleidae (0.9%) and Elopidae (0.7%).

The most abundant larvae were those of the thorny anchovy, *S.holodon*, and Gobiid 12 (32.1% and 29.7% of the total catch, respectively). In order of abundance the following species were also relatively abundant: *T.vitrirostris* (17.8%), *Taenioides esquivel* (4.1%) and *Pellona ditchela* (2.9%). The larvae of *H.quadrimaculatus* and *Croilia mossambica* each contributed 1 - 2% of the total catch (Table 5.1).

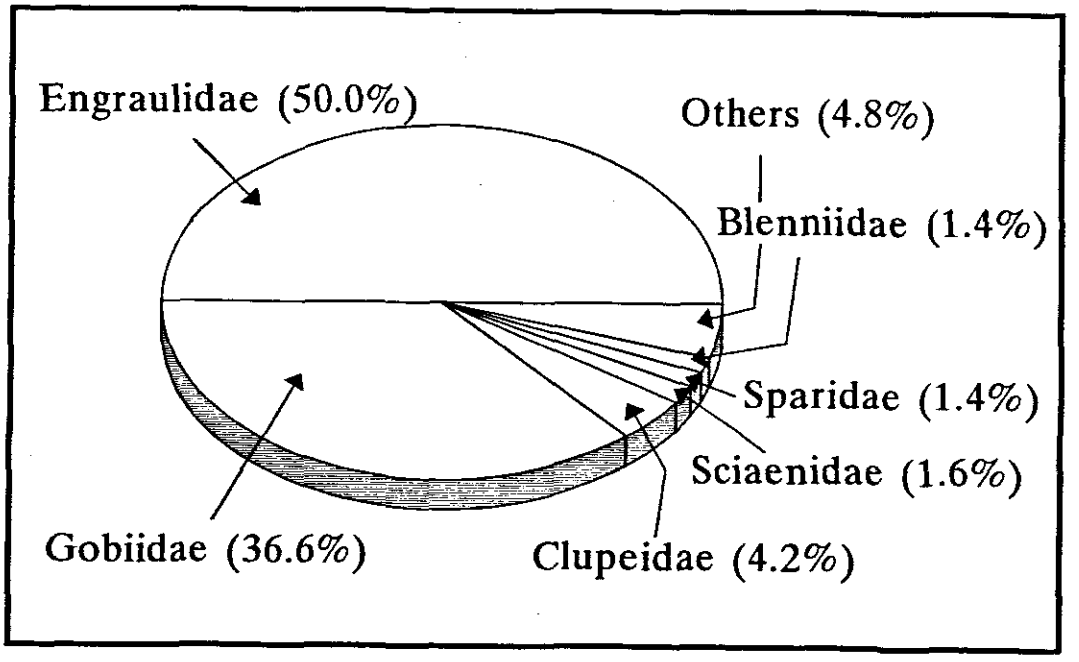


Figure 5.2. Percentage contribution of dominant families for all taxa collected in the study.

Table 5.1. Total catch, body length, developmental stage and estuarine-association category for all larval and juvenile fish taxa collected in Richards Bay Harbour. (Gl, glass eel; Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile; Ad, adult; F, flood tide; E, ebb tide - *abundant; **very abundant)

Family	Species	Rank overall	Total catch no	Total catch mean no.100m^{-3}	%	Body length (mm) mean	Body length (mm) range	Developmental stage	Presence	Ju/Ad present[A]
ESTUARINE-DEPENDENT										
Catadromous										
Anguillidae	*Anguilla mossambica*		1	<0.01	<0.1	48.0		Gl	E	
Estuarine residents										
Clupeidae	*Gilchristella aestuaria*		1	<0.01	<0.1	24.0		Ju	E	+
Gobiidae	*Redigobius* sp.		12	0.04	0.1	4.1	2.0-7.0	Pr,Fl,Po	F,E	
	Taenioides jacksoni		3	0.01	<0.1	10.0		Po	F,E	
Eleotridae	Eleotrid 2		7	0.02	0.1	14.4	13.0-15.0	Po	F,E	
Marine spawners dependent on estuaries										
Elopidae	*Elops machnata*	11	49	0.20	0.7	32.2	26.0-37.0	Le	F, E	+
Engraulidae	*Thryssa vitrirostris*	3	1110	5.22	17.8	10.0	4.0-22.0	Pr,Fl,Po	F**,E**	+
Teraponidae	*Terapon jarbua*		3	0.01	0.0	6.0	5.0-7.0	Fl,Po	F,E	+
Haemulidae	*Pomadasys commersonnii*	19	28	0.11	0.4	11.0	7.0-13.0	Po	F*,E	+
Sparidae	*Rhabdosargus holubi*	12	52	0.18	0.6	9.4	6.5-11.0	Po	F*,E	+
	Acanthopagrus berda	15	34	0.14	0.5	8.2	6.0-11.0	Fl,Po	F,E	+
	Rhabdosargus sarba	20	25	0.11	0.4	6.4	2.0-10.5	Pr,Fl,Po	F,E	+
PARTIALLY ESTUARINE-DEPENDENT										
Catadromous										
Megalopidae	*Megalops cyprinoides*		3	0.01	<0.1	24.3	24.0-25.0	Le	F	
Estuarine and marine spawners										
Atherinidae	*Atherinomorus lacunosus*		1	<0.01	<0.1	16.5		Po	F	
Syngnathidae	*Hippichthys heptagonus*		6	0.03	0.1	19.5	7.0-35.0	Po,Ju	F,E	
Ambassidae	*Ambassis* sp.		11	0.06	0.2	5.8	3.0-13.0	Fl,Po	F,E	+
Gobiidae	*Croilia mossambica*	7	77	0.30	1.0	10.2	4.5-14.0	Po	F*,E	
	Taenioides esquivel	4	287	1.21	4.1	4.3	3.0-11.0	Pr,Fl,Po	F**,E*	
	Trypauchen microcephalus		2	0.01	<0.1	51.0	50.0-51.0	Ju	E	

cont.

Table 5.1. cont.

Marine spawners with juveniles abundant in estuaries									
Sciaenidae	*Argyrosomus* sp.		20	0.08	0.3	6.8	3.5-17.0	Pr,Fl,Po	F,E	+
Mugilidae	Mugilid spp.		3	0.01	<0.1	10.0	9.5-11.0	Po	F	+
Soleidae	*Solea bleekeri*	10	57	0.25	0.9	4.4	3.0-7.0	Pr,Fl,Po,Ju	F*,E	+
Marine spawners with juveniles at sea and in estuaries									
Engraulidae	*Stolephorus holodon*	1	2435	9.40	32.1	12.2	4.8-31.0	Pr,Fl,Po,Ju	F**,E**	
Chanidae	*Chanos chanos*		4	0.03	0.1	12.0	11.5-12.5	Po	F,E	
Platycephalidae	*Platycephalus indicus*		5	0.02	0.1	7.7	5.0-10.0	Fl,Po	F,E	+
Gerreidae	*Gerres* sp.1		3	0.01	<0.1	4.6	4.0-5.0	Pr,Fl	F,E	+?
Sillaginidae	*Sillago sihima*		8	0.03	0.1	12.4	9.0-15.0	Po	F,E	+
Sciaenidae	*Johnius dussumeiri*	9	69	0.26	0.9	5.0	2.5-15.5	Pr,Fl,Po	F*,E*	+
Leiognathidae	*Leiognathus equula*		6	0.02	0.1	7.8	6.5-9.0	Po	F,E	+
ESTUARINE-INDEPENDENT[B]									
Reef and shore taxa									
Clupeidae	*Pellona ditchela*	5	262	0.85	2.9	11.9	8.0-22.0	Pr,Fl,Po	F**,E**	
	Herklotsichthys quadrimaculatus	6	82	0.33	1.1	11.3	4.8-20.0	Pr,Fl,Po	F*,E*	
Sciaenidae	Sciaenid 2	16	32	0.13	0.4	6.0	3.0-14.0	Pr,Fl,Po	F*,E	
Blenniidae	Blenniid 1	8	74	0.28	1.0	3.8	2.0-6.0	Pr,Fl,Po	F*,E*	
	Omobranchus sp.	17	35	0.12	0.4	3.9	2.5-6.0	Pr,Fl	F*,E	
Callionymidae	*Draculo celatus*	13	40	0.16	0.5	4.5	2.0-12.0	Pr,Fl,Po	F*,E	
Gobiidae	Gobiid 12	2	2074	8.70	29.7	4.8	2.5-12.0	Pr,Fl,Po	F**,E**	
	Gobiid 13	18	31	0.11	0.4	3.3	3.0-3.8	Pr	E	
	Gobiid 27		21	0.08	0.3	4.7	2.0-10.5	Pr,Po	F,E	
	Gobiid 28	14	31	0.14	0.5	3.7	3.0-6.0	Pr,Fl,Po	F,E	

Total number of larvae = 7163
Total number of taxa = 105
Total number of families = 53

[A]Millard and Harrison (1954); van der Elst (1974-1986); Hay *et al*. (1993)
[B]taxa contributing < 0.3% of the total catch are listed in Appendix III

Multiple regression analysis for each estuarine-association group of larvae and the most abundant species of larvae in each group showed that different combinations of the environmental variables accounted for some of the variability in larval densities (Table 5.2). Turbidity and temperature were both significant variables explaining 27% of the regression model for estuarine-dependent species, particularly for the engraulid *T.vitrirostris*. Turbidity was also a significant factor for partially dependent species, in addition to salinity, although both variables together only accounted for 8% of the variation in larval densities. Of the two most abundant species partially dependent on estuaries, only *T.esquivel* showed a significant relationship to environmental variables (Table 5.2). For species not dependent on estuaries temperature, turbidity and salinity together explained 27% of the variance.

Table 5.2. Stepwise regression statistics of larval fish densities versus environmental variables (sa, salinity; te, temperature; tu, turbidity) for each estuarine-association group and the most abundant species in each group, in Richards Bay Harbour. (adj; adjusted R^2; coefficient of determination; R, correlation coefficient; F, F statistic; –, adjusted $R^2 = 0$)

Estuarine-association group	adjR^2	R	F	significant variables
All taxa	0.17	0.41	22.26***	tu***; sa***
Estuarine-dependent	0.27	0.52	38.44***	tu***; te***
Thryssa vitrirostris	0.36	0.60	59.64***	tu***; te***
Partially estuarine-dependent	0.08	0.28	10.38***	tu***; sa**
Taenioides esquivel	0.17	0.41	22.15***	tu***; sa**
Stolephorus holodon	–	–	–	–
Estuarine-independent	0.27	0.52	26.69***	te***; tu***; sa***
Gobiid 12	0.33	0.57	34.78***	te***; sa***; tu***
Pellona ditchela	0.18	0.42	23.57***	te***; tu**

P<0.05; **P<0.01;***P<0.001

5.2.3. Estuarine-Association

Marine spawners which are not dependent on estuaries (categories IIIa and IIIb) comprised 72.4% of all taxa collected, but did not dominate in terms of total density (Figure 5.3). A total of 28 taxa, which are dependent on estuaries to some degree, was recorded and dominated the catch in terms of density (60.7%). Eleven of the 28 taxa are

totally dependent on estuaries at some stage in their life cycle and comprised 20.6% of the total density. Two catadromous species were recorded, *Megalops cyprinoides* and *Anguilla mossambica* but only a few individuals of each species were collected (see Table 5.1).

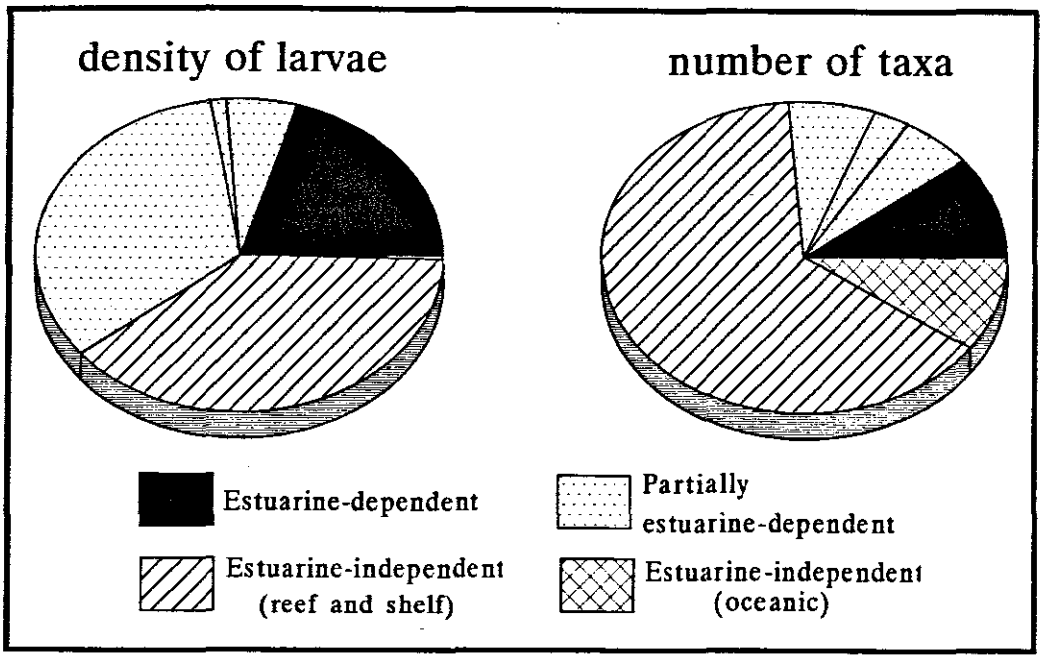


Figure 5.3. Percentage contribution of the estuarine-association categories, in terms of density of larvae and number of taxa, for all taxa sampled in the study.

5.2.4. Temporal and Spatial Trends in Larval Fish Density

The main peak in larval density, which occurred in January 1992, was as a result of larvae of both estuarine-dependent species (70 larvae per $100m^3$ - mainly Gobiid 12) and estuarine-independent species (89 larvae per $100m^3$ - mainly *T.vitrirostris*) being abundant (Figure 5.4B and D, and Figure 5.5). Mean larval density of estuarine-dependent species for the remaining sampling dates did not exceed 7 larvae per $100m^3$. A second, smaller peak in larval density of estuarine-independent taxa occurred in October 1992 (32 larvae per $100m^3$) which was also from an abundance of Gobiid 12 in that month (Figure 5.5). Mean larval densities of partially estuarine-dependent taxa were highest in August 1992 (65 larvae per $100m^3$) and lowest in June 1992 (0.3 larvae per $100m^2$) (Figure 5.4C). Larvae from the partially dependent group were also relatively abundant in October and November 1992 (29 larvae per $100m^3$). The peak in abundance in August, October and November 1992 was because larvae of *S.holodon* (partially estuarine-dependent) were abundant for those three months (Figure 5.5).

Only larval densities of the partially dependent group differed significantly with tide ($P < 0.05$) with densities being higher on flood tides (Table 5.3). Depth was a main effect with larval densities of all groups and most of the individual abundant species being significantly higher in mid and bottom samples. Note that the mean squares for depth were greatest for the partially dependent group and for *S.holodon*, indicating a greater significance. Month was also a dominant effect with relatively high mean squares indicating distinct seasonal differences in larval abundance. The tide x depth interaction was only significant for Gobiid 12 ($P = 0.003$). Only three of the abundant species (*T.esquivel, S.holodon* and Gobiid 12) had significant tide x month interactions, whilst, all the abundant species in each group had significant depth x month interactions (Table 5.3).

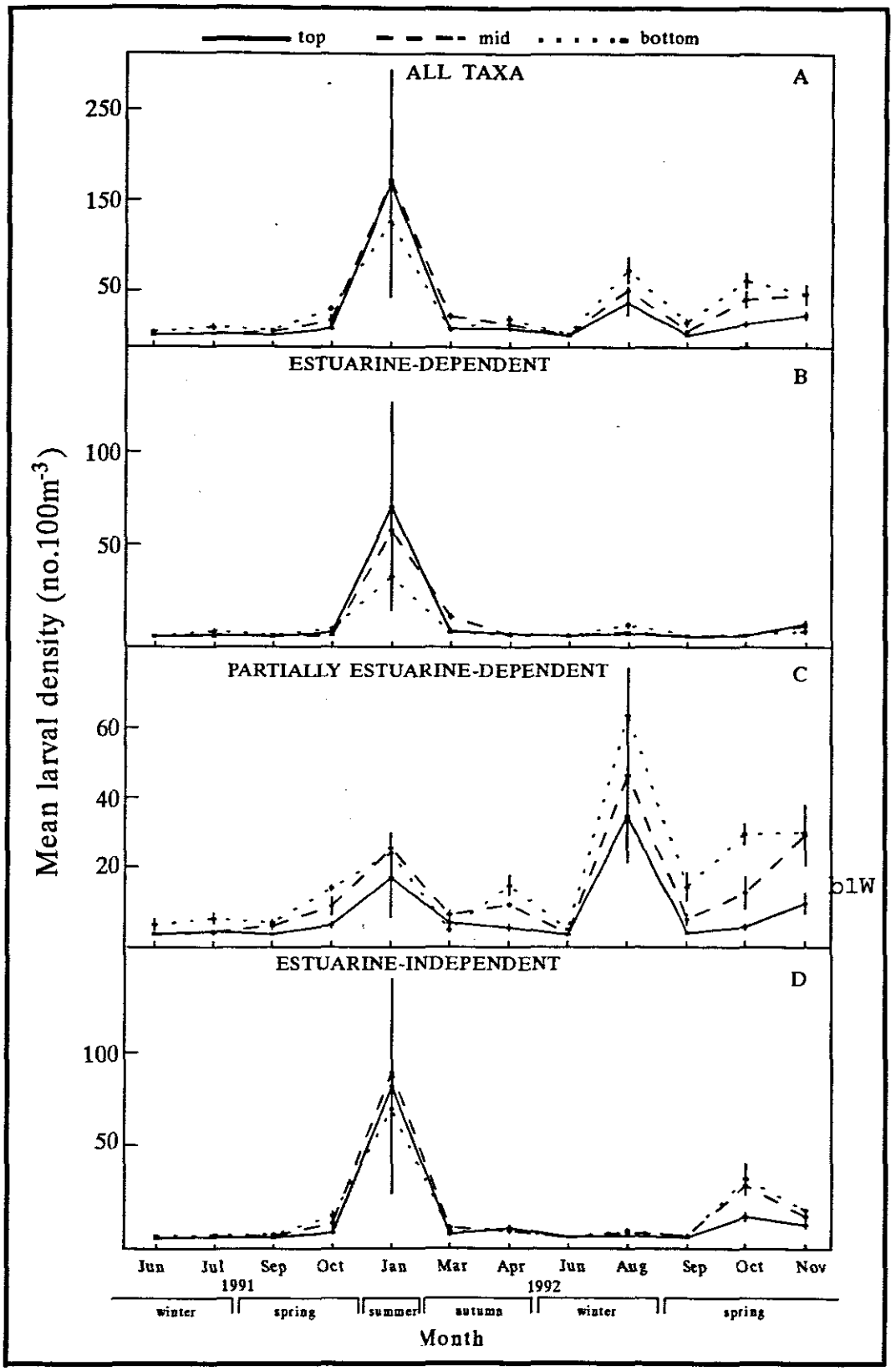


Figure 5.4. Mean monthly variations in larval densities (± 1SE) in top, mid and bottom samples for all taxa together (A), estuarine-dependent taxa (B), partially estuarine-dependent taxa (C) and estuarine-independent taxa (D).

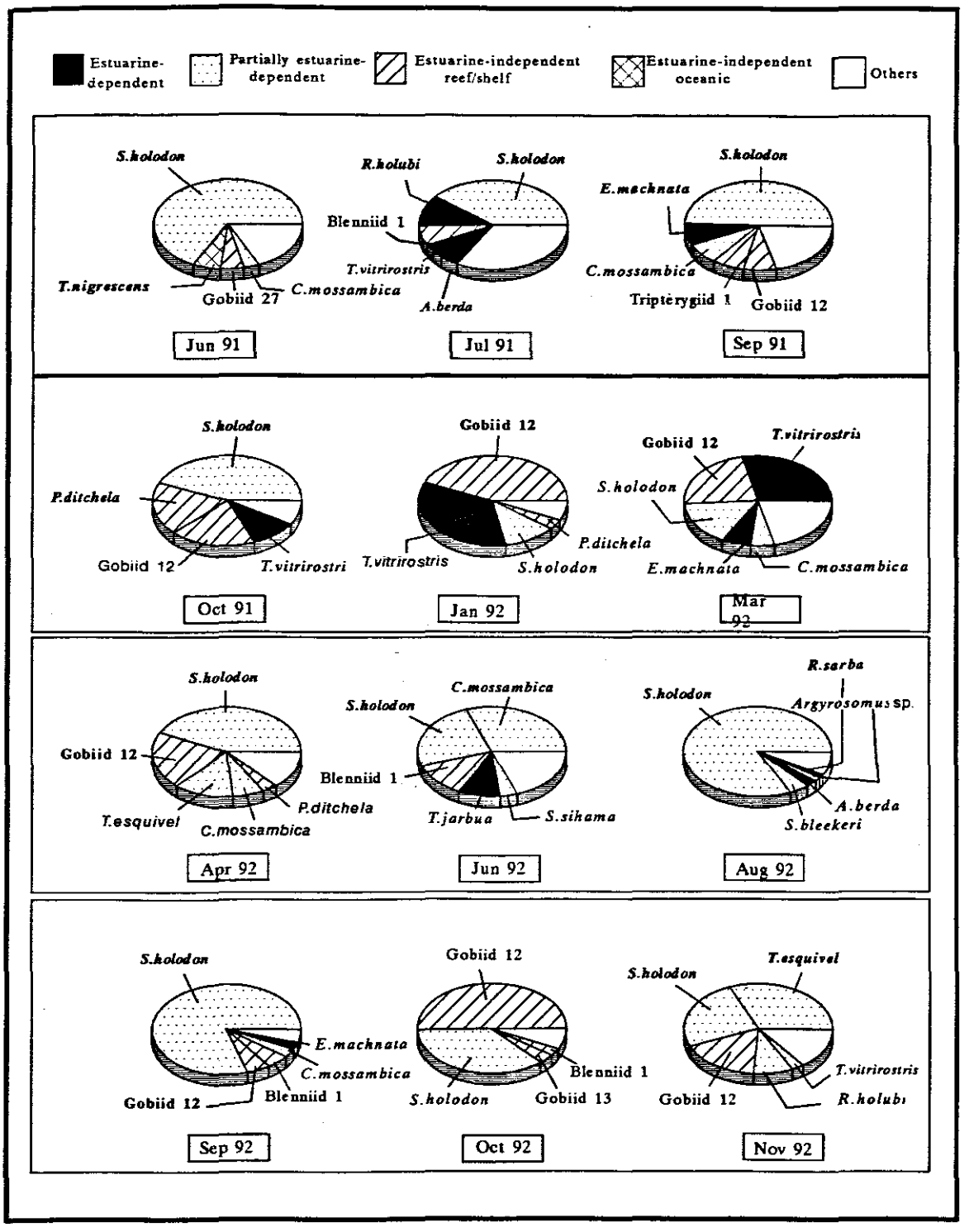


Figure 5.5. Percentage contribution of the most abundant species in the total catch sampled each month in Richards Bay Harbour.

Table 5.3. Mean squares and significance levels for three-way ANOVA of densities of the most abundant species in each estuarine-association group. (DF = degrees of freedon)

Estuarine-association group	Main effects			2-way interactions		
	Tide (F/E)[A] (DF=1)	Depth (T,M,B)[B] (DF=2)	Month (1 to 12)[C] (DF=11)	Tide x Depth (DF=2)	Tide x Month (DF=11)	Depth x Month (DF=22)
All taxa	0.14	3.14***(B>M>T)	5.29***	0.17	0.13	0.18*
Estuarine-dependent	0.002	0.25*(B>T)	3.07***	0.05	0.11	0.18***
Thryssa vitrirostris	0.01	0.01	3.36***	0.03	0.05	0.15***
Partially estuarine-dependent	0.32*(F>E)	4.00***(B>M>T)	3.34***	0.08	0.10	0.22***
Taenioides esquivel	0.06*(F>E)	0.08**(BM>T)	1.12***	0.02	0.04**	0.04***
Stolephorus holodon	0.11	4.06***(B>M>T)	3.14***	0.14	0.17*	0.23***
Estuarine-independent	0.13	1.24***(BM>T)	4.28***	0.23	0.12	0.09
Gobiid 12	0.09	0.65***(BM>T)	4.51***	0.44**	0.17**	0.18***
Pellona ditchela	0.01	0.30***(BM>T)	0.87***	0.05	0.03	0.09***

*P<0.05;**P<0.01;***P<0.001

[A]tide where densities are highest is indicated in parentheses. F, flood tide; E, ebb tide

[B]depths where demities are highest are indicated in parentheses and Fig. 5.4 (Groups only). T, top; M, mid; B, bottom

[C]months where denities are highest is indicated in Fig. 5.4 (Groups only)

5.2.5. Developmental Stages

Young larvae (preflexion and flexion) were relatively abundant in all the estuarine-association groups (Figure 5. 6). Old larvae (postflexion) were most abundant in the partially estuarine-dependent group (60.7% of the total catch). A few juveniles were present in all three groups (see Table 5.1). The leptocephali and glass eel stages in the catadromous category belonged to the oxeye tarpon *M.cyprinoides* and the longfin eel *A.mossambica*. The estuarine-independent taxa were mainly present as young larvae (preflexion and flexion - 54% of the total).

Postflexion larvae predominated in most months sampled except January, August and November 1992 (Figure 5.7). Flexion stages were particularly abundant in January and August 1992 (Figure5.7) since engraulids (*T.vitrirostris* and *S.holodon*) were abundant in both those months (Figure 5.5). Leptocephalus larvae were present in all months sampled, but particularly in September 1991 and March 1992, and were mainly due to the presence of *Elops machnata* but also *M.cyrinoides* and eel species. Juveniles were present in September 1991 and January, April and June 1992.

Proportions of developmental stages varied with tide and with depth and was species-specific (Figure 5.8). Preflexion larvae of the eelgoby, *T.esquivel,* were more prevalent on flood tides than on ebb tides suggesting a net input into Richards Bay Harbour from a marine spawning population. Larvae of *T.vitrirostris* were predominantly flexion stages which were most abundant in mid waters on the ebb tide. Postflexion larvae of *S.holodon* were particularly abundant in bottom waters on the flood tide, with the least number of larvae in top samples on both flood and ebb tides. Note that juveniles of *S.holodon* were only collected in bottom samples on both the flood an ebb tide. Larvae of the sciaenid *J.dussumeiri*, were most abundant on ebb tides with postflexion stages being prevalent. In fact, only a few preflexion larvae were collected in top samples on both ebb and flood tides. Preflexion, flexion and postflexion stages of the clupeid, *P.ditchela,* were present on both flood and ebb tides with most larvae being present in mid and bottom waters. Larvae of Gobiid 12 were present also at all three stages of development and with more larvae in mid and bottom waters, particularly on ebb tides (Figure 5.8).

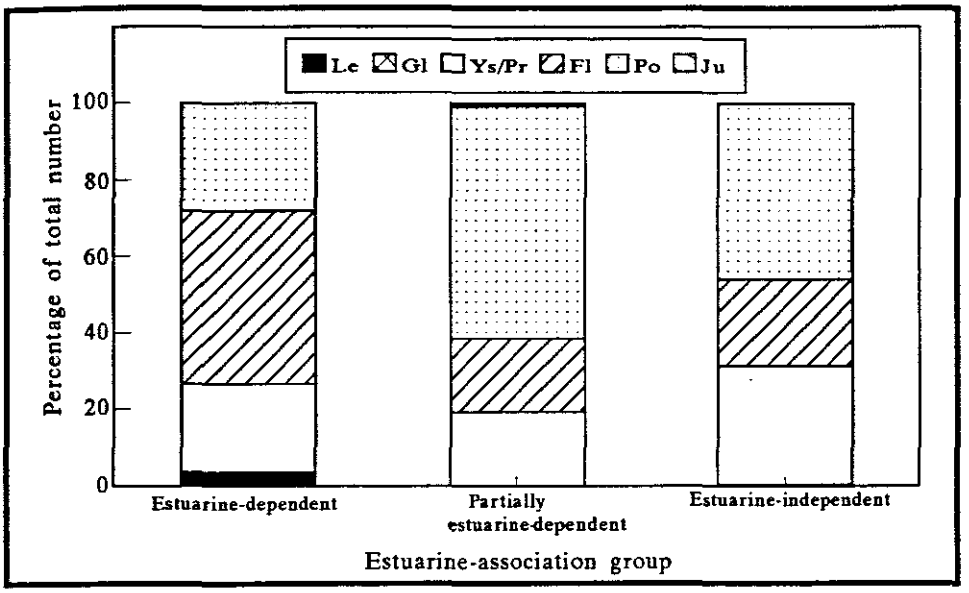


Figure 5.6. Percentage composition of the different developmental stages of all larvae for each estuarine-association category. Gl, glass eel; Le, leptocephali; Ys, yolk sac; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile.

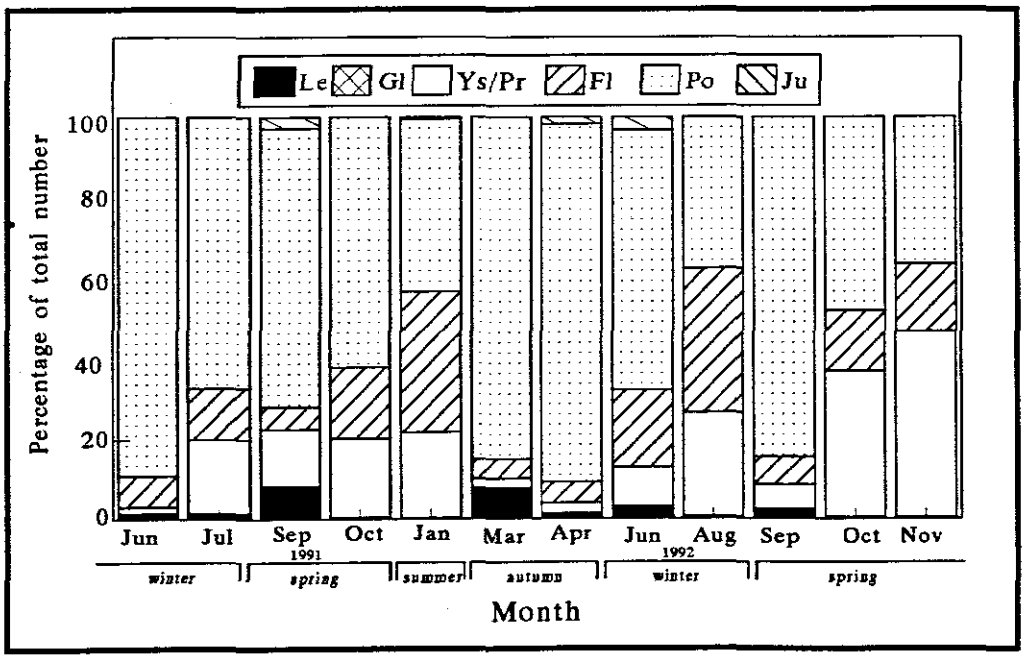


Figure 5.7. Monthly percentage composition of developmental stages of all larvae sampled in the study. Gl, glass eel; Le, leptocephali; Ys, yolk sac; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile.

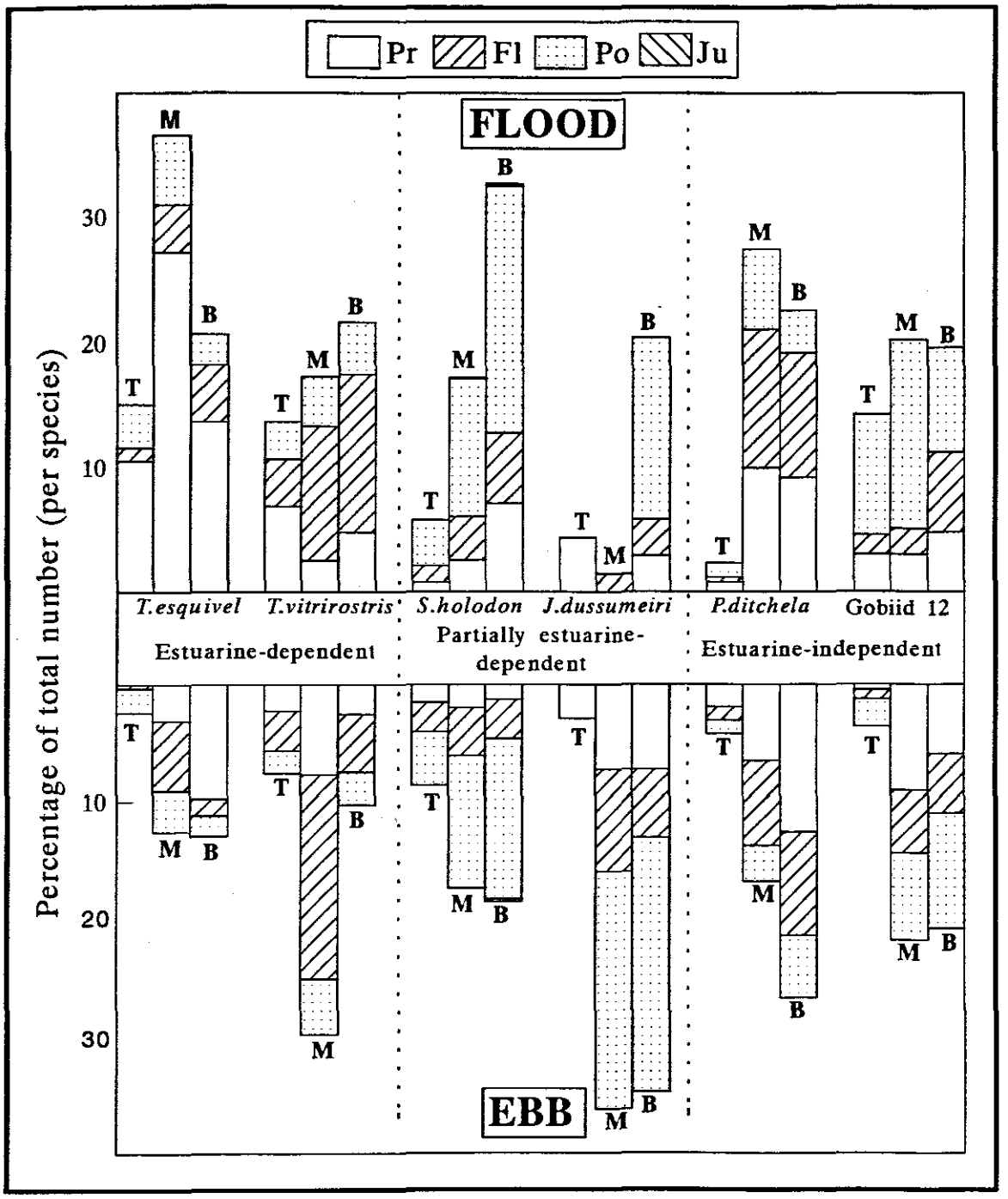


Figure 5.8. Percentage composition of developmental stages for the most abundant species in each estuarine-association group, on flood and ebb tides for the study period.(T, top; M, mid; B, bottom)

5.3. Discussion

5.3.1. Composition of the Larval Assemblage

The dominance of the Clupeiformes and Gobiidae in the larval assemblage in Richards Bay Harbour is typical of other temperate and subtropical estuaries and bays in the southern hemisphere (Melville-Smith and Baird 1980; Jenkins 1986; Roper 1986; Whitfield 1989a; Gaughan *et al.* 1990; Harrison and Whitfield 1990; Neira *et al.* 1992; Neira and Potter 1994). The most abundant species in these estuarine environments are usually estuarine-associated species, either totally or partially dependent on estuaries. For example, in the Nornalup-Walpole Estuary in southwestern Australia the most abundant species were an engraulid (*Engraulis australis*) and two gobiid species (*Pseudogobius olorum* and *Favonigobius lateralis*) with all three species being estuarine spawners (Neira and Potter 1994). Although larvae in the families Clupeidae and Gobiidae also dominated the ichthyoplankton in Durban Harbour (see Figure 4.2, Chapter 4), the dominant species in those families were marine stragglers (*H.quadrimaculatus* and Gobiid 12) and therefore not associated with estuaries. The composition of fish larvae in Richards Bay Harbour is intermediate from a "typical" estuary, like the St Lucia Estuary (Chapter 6) and a marine-dominated habitat, like Durban Harbour (Chapter 4), since both estuarine- and marine-associated species dominated the catch (Table 5.1). It is interesting to note that larvae of the clupeid *P.ditchela* (Indian pellona) were relatively abundant in Richards Bay Harbour (ranked 5th overall) but was not recorded at all at any of the other study sites along the KwaZulu-Natal coast (see Appendix I). This species is widespread in shallow coastal waters (4 to 20 m depths), estuaries and lagoons of the Indo-Pacific (Fischer and Bianchi 1984) and is usually caught in the same hauls as *T.vitrirostris* in the shrimp fisheries by-catch at the Sofala Bank and in Maputo Bay off the Mozambique coast (Gislason and Sousa 1985; see Figure 2.1, Chapter 2 for location).

Whitfield (1994a) listed a total of 20 gobiid species, which occur in the subtropical region of southern Africa, as being dependent on estuaries. Of those 20 species, seven species have been identified as larvae in the present study with the remaining gobies being unidentified (Appendix I). It is possible that the abundant unidentified gobies in Durban and Richards Bay Harbours are estuarine-dependent

species but these gobies were present also in the nearshore marine environment adjacent to the St Lucia Estuary (Table 9.2, Chapter 9) and so have been placed in the estuarine-independent category.

Fish surveys of Richards Bay, prior to the development of the harbour, found an abundance of juveniles of marine species with some degree of estuarine-dependence (Millard and Harrison 1954; Wallace and van der Elst 1975; Begg 1978). Subsequent studies show that Richards Bay Harbour still functions as an important nursery area for many marine fish species, in particular, *T.vitrirostris, Gerres* sp., *R.sarba, Ambassis* sp., *A.berda, Sillago sihama* and mullet species (Cyrus *et al.* 1992; Hay 1993). Larvae of all these species were collected in Richards Bay Harbour during the present study, *T.vitrirostris* ranking third overall (Table 5.1).

The larval fish assemblage in Richards Bay Harbour was predominantly marine species (72.4% of total catch) which is similar to Durban Harbour (81% of total catch). In terms of density, however, Richards Bay Harbour had a greater proportion of estuarine-associated species than Durban Harbour (Figure 4.3 - Chapter 4, and Figure 5.3). Of the 105 taxa collected in the present study, 20 species have been recorded as juveniles and/or adults in the harbour (Millard and Harrison 1954; van der Elst 1975-1986. Hay *et al.* 1995). Seventeen of the 20 species (85%) are fish species dependent or partially dependent on estuaries (categories I and II) and were collected at larval stages in this study, for example *T.vitrirostris, E.machnata* and *A.berda.* The juveniles or adults of engraulids (e.g. *S.holodon*) and gobies (e.g. *T.jacksoni*), which have not been recorded in Richards Bay Harbour but were abundant as larvae, suggests that the methods of sampling in previous fish surveys (seine and gill netting) missed certain pelagic and benthic species.

Tidal exchange is the most important factor controlling the zooplankton in the Richards Bay system (Begg 1978). A survey of the plankton in Richards Bay was carried out in 1970 (Grindley and Wooldrige 1974) which showed that two distinct communities were present: (1) a diverse neritic community in the tidally influenced areas (2) a copepod dominated estuarine community in the western section of the sanctuary (see Figure 2..3, Chapter 2). This parallels the situation found in the present study and in Durban Harbour where the ichthyoplankton community is composed of both a neritic

marine community and an estuarine community, suggesting that tidal exchange plays a role in influencing the composition of the larval assemblages in these two systems.

5.3.2. Larval Fish Abundance in Relation to Environmental Conditions

Prior to the development of Richards Bay into a harbour, a salinity gradient existed along the length of the bay (Millard and Harrison 1954; Begg 1978). The bay was shallow with a muddy bottom (0.9 m deep) and extensive beds of the seagrass *Zostera capensis* supported a diverse estuarine community (Begg 1978; Day 1981c - see Figure 2.3A, Chapter 2). These environmental conditions were, therefore, very suitable for estuarine-associated fish species to inhabit. The prevailing water conditions in the harbour section of the bay are somewhat different today with salinities being essentially marine and with low turbidities near the entrance channel. High turbidities, do however, still persist in the southern mangrove area near the berm wall (see Figure 2.3B, Chapter 2). Despite these changes, many estuarine-associated fish species still recruit into the harbour which indicates there are sufficient environmental cues attracting fish to the area. Compared with Durban Harbour, average turbidities in the present study were generally higher (compare Figure 4.1 - Chapter 4 and Figure 5.1) with turbidity being the most significant factor influencing larval fish abundance of estuarine-dependent species ($P < 0.001$). Turbidity may, therefore, provide a cue for recruiting fish larvae of estuarine-dependent species, such as *T.vitrirostris,* recruiting into the harbour.

The presence of larvae of marine stragglers in estuarine habitats has been attributed to pulses of nearshore and oceanic water entering the system (Miskiewicz 1987). In southwestern Australia, Neira and Potter (1994) found that larvae of marine species were present in the entrance channel of the Nornalop-Walpole Estuary and suggested that they were passively transported into the Estuary on flood tides. Since these larvae were predominantly at the preflexion stage, the authors surmised that the larvae probably do not survive once in the estuarine environment. A similar situation may apply to both Richards Bay Harbour and Durban Harbour which have moderately deep entrance channels with a constant tidal exchange. Larvae of a number of different reef-, shelf- and oceanic-associated taxa were present the present Richards Bay Harbour

study (Appendix III), but more so in Durban Harbour (Appendix II) and probably also do not survive in the bay unless they are washed back out to sea on the ebb tides.

5.3.3. Temporal and Spatial Trends in Abundance of Fish Larvae

The summer peak in larval fish abundance in Richards Bay Harbour is characteristic of other estuaries in the southern hemisphere (Melville-Smith and Baird 1980; Whitfield 1989a; Harrison and Whitfield 1990; Neira and Potter 1994). However, different species in different estuarine systems cause these peaks in abundance and thus depends on how "estuarine" a system is i.e. the environmental conditions of that system. For example, in Durban Harbour peaks in abundance are from marine straggler species whereas in St Lucia Estuary the dominant peaks are from estuarine spawners (Figure 6.5, Chapter 6).

The small pelagic species *T.vitrirostris* and *P.ditchela* are usually caught together and recruitment on the Mozambique coast takes place April to June (Sofala Bank) and in September to October (Maputo Bay) (Gislason and Sousa 1985). Larvae of these two species similarly occurred together in the present study and were most abundant in the October 1991 and January 1992 samples (Figure 5.5). This suggests a similar spawning strategy persists on the KwaZulu-Natal coast but the location of the marine spawning grounds is not known. Since a large proportion of the larvae in those two months were young larvae, this suggests the spaning ground is in close proximity to the harbour entrance. However, spawning of *T.vitrirostris* has been recorded within the St Lucia estuarine-lake system (Blaber 1979)..

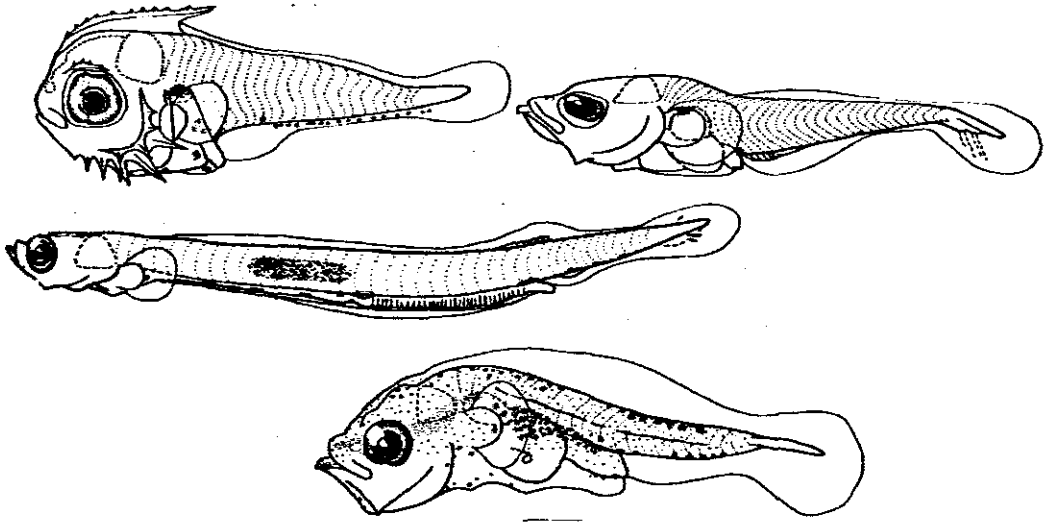
5.3.4 Developmental Stages

The size at which larvae of estuarine-associated fish species, which spawn in marine waters, enter an estuarine nursery habitat is indicative of the proximity of spawning grounds (Miskiewicz 1986). Similar patterns in tidal exchange of larvae occurred in Richards Bay Harbour compared with Durban Harbour. This is to be expected since both systems have wide and deep entrance channels and so are deep enough for fish larvae to migrate up and down in the water column. Of particular note is the eel goby

T.equivel, an estuarine-dependent species which spawns in estuaries. The larvae this goby were most abundant on flood tides suggesting a net input of larvae into the harbour.

CHAPTER 6

The Larval Fish Assemblage in the St Lucia Estuary



6. THE LARVAL FISH ASSEMBLAGE IN THE ST LUCIA ESTUARY

6.1. Introduction

Research on southern African estuarine fish populations has been directed primarily at the juvenile and adult life stages (Wallace 1975a,b; Wallace and van der Elst 1975; Blaber 1980; Beckley 1984; Wallace *et al.* 1984: Cyrus and Blaber 1987a,b; Bennett 1989a; Whitfield and Kok 1992). This research has shown that estuaries in southern Africa play a very important role as nursery areas for the juvenile stages of many fish species. An understanding of the early life histories of estuarine-associated fishes is, however, important if the utilisation of estuaries as nursery areas by the juveniles of these species is to be placed in context (Whitfield 1989a). Larval fish studies in South African estuaries have been concentrated in the Western and Eastern Cape in the Swartkops (Melville-Smith and Baird 1980; Beckley 1985), Kromme (Melville-Smith 1981), Swartvlei (Whitfield 1989a), and Sundays estuaries (Harrison and Whitfield 1990). A recent study by Whitfield (1994c) investigated abundance of larval and 0+ juvenile marine fishes in Great Fish, Sundays and Kariega estuaries. Some research on larval fish in the St Lucia Estuary, KwaZulu-Natal, has been undertaken. However, the first study (Wallace 1975a) only gives a brief description of species composition and the second study used a 1mm mesh net and thus sampled mainly juveniles (Martin *et al.* 1992).

Marine fish species utilizing estuaries as nursery areas are recruited at an early life history stage, particularly during the postflexion larval developmental stage (Melville-Smith and Baird 1980; Miskiewicz 1987; Whitfield 1989a,b,c; Gaughan *et al.* 1990; Harrison and Whitfield 1990; Neira *et al.* 1992; Tzeng and Wang 1992; Warlen 1994; Whitfield 1994c). The ichthyoplankton of estuaries can either result from spawning within the estuary or from early life history stages entering the estuary from the sea (de la Fontaine 1990). The different ways in which fishes utilize estuaries have been variously categorised (McHugh 1967; Dando 1984; Wallace *et al.* 1984; Miskiewicz 1987; Loneragan and Potter 1990; Neira *et al.* 1992; Whitfield 1994a,b). Although the majority of fishes found in estuaries are those of species that spawn at sea, there are also a few species that complete their entire life cycle in estuaries (Haedrich

1983; Dando 1984; Claridge *et al.* 1986). The size of fish species entering an estuarine nursery ground from offshore indicates the length of time spent at sea and hence the proximity of spawning grounds (Miskiewicz 1986).

St Lucia, the largest estuarine system in Africa (Blaber 1985; see Figures 2.1 and 2.4, Chapter 4), has a very diverse ichthyofauna because of the shallow turbid nature of the system and good connection with the sea (Wallace and van der Elst 1975; Whitfield 1980; Blaber 1985). Ten years, ago Wallace *et al.* (1984) divided the estuarine-associated fish fauna of South Africa into six categories. Whitfield (1994a,b) recently revised their classification system (see 3.2.3, Chapter 3) and recognised five major types of estuarine dependence. The aim of the present study was to determine recruitment patterns of larval stages of fish by examining the species composition and estuarine-association of all taxa sampled. In addition, seasonality and developmental stages of the larvae were examined.

6.2. Results

6.2.1. Environmental Variables

During the study period, from November 1987 to October 1988, monthly variations in the environmental variables occurred at the sample site (see Figure 2.4, Chapter 2) in the St Lucia Estuary (Figure 6.1). For the months that current velocity was measured (from May to October 1988) actual values ranged from 0.2 to 0.7 ms^{-1} and was variable within the same sampling period depending on the state of the tide. Current velocity was significantly higher in top samples ($F = 16.84$; $P = 0.0001$) and between sampling dates ($F = 11.8$; $P < 0.0001$).

No consistent seasonal trend was found for salinity with mean monthly salinity being both minimal and maximal in summer (December - 7.7 ‰; February - 34.5 ‰) and in autumn (April - 8.1 ‰; May2 - 32.7 ‰) (Figure 6.1). Salinity was significantly higher in bottom samples ($F = 17.8$; $P < 0.0001$) and differed significantly between sampling dates ($F = 51.6$; $P < 0.0001$).

Small variations in mean monthly water temperature occurred with the minimum and maximum value being 18.8°C in winter (June) and 28.8°C in late summer (March), respectively (Figure 6.1). No significant differences between top and bottom

temperatures were found (F = 0.6; P = 0.45) but there were significant monthly differences (F = 373.1; P < 0.0001).

Mean monthly turbidity peaked in November (208 NTU) and March (184 NTU) and decreased to a minimum during May and June (26 and 27 NTU, respectively) (Figure 6.1). Turbidity was significantly higher in bottom samples (F = 37.5; P < 0.0001) and between sampling dates (F = 25.7; P < 0.0001).

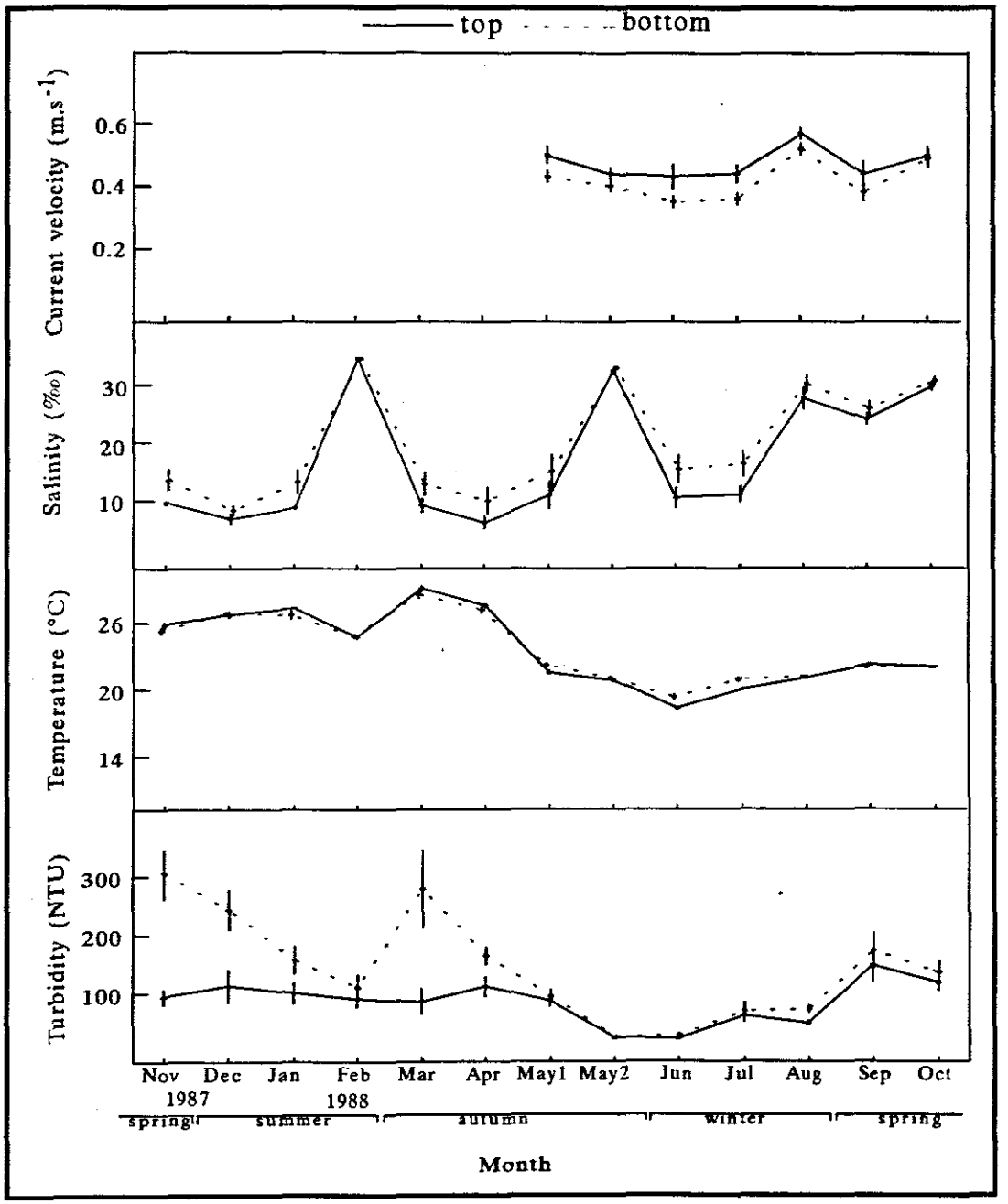


Figure 6.1. Mean monthly variations (± 1SE) of the environmental variables (salinity, temperature and turbidity) for top and bottom samples in St Lucia Estuary for the study period.

6.2.2. Assemblage Composition and Relationships to Environmental Variables

A total of 51 690 fish larvae, representing 44 families and 85 taxa, was collected between November 1987 to October 1988 (Table 6.1). Gobiidae was by far the most dominant family comprising 74.5% of the total number of larvae, followed by the Clupeidae (18.9%) and Engraulidae (2.2%) (Figure 6.2). The only other families contributing more than 0.5% were the Elopidae (0.9%), Soleidae (0.7%) and Ambassidae (0.6%).

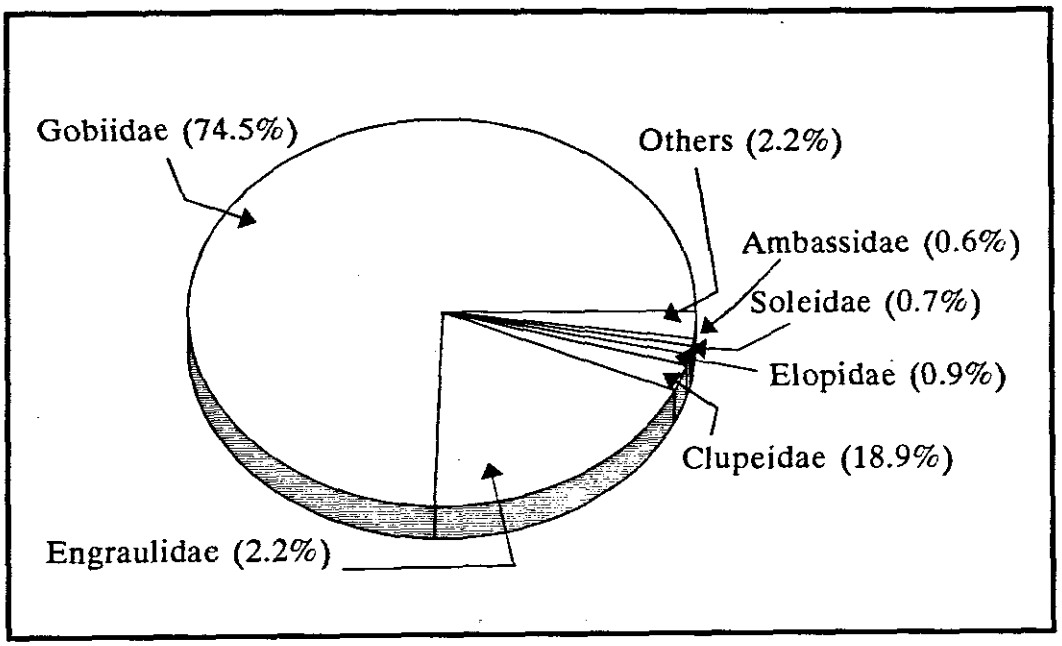


Figure 6.2. Percentage contribution of dominant families for all taxa collected in the study.

The most abundant species were the goby *Glossogobius callidus* and the clupeid *Gilchristella aestuaria* which accounted for 67.2% and 18.9 % of the total, respectively. These species were followed in order of relative abundance by *C.mossambica* (4.4%), *T.esquivel* (1.4%), *T.vitrirostris* (1.3%), *S.holodon* (1.0%), and *E.machnata* (0.9%). The larvae of *T.jacksoni*, *S.bleekeri*, *Ambassis* sp., *R.holubi*, *L.equula*, *J.dussumieri*, *T.jarbua*, *M.cyprinoides*, Eleotrid 2 and Gobiid 4 each contributed between 0.2 - 0.8% of the total (Table 6.1).

Table 6.1. Total catch, body lengt and developmental stage all larval fish taxa collected in The St Lucia Estuary.
(Gl, glass eel; Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile; Ad, adult)

Family	Species	Rank overall	Total catch no	Total catch mean no.100m^{-3}	%	Body length (mm) mean	Body length (mm) range	Developmental stage	Ju/Ad present[A]
ESTUARINE-DEPENDENT									
Catadromous									
Anguillidae	*Anguilla mossambica*		6	0.03	<0.1	57.9	49.0-62.0	Gl	+
Estuarine residents									
Clupeidae	*Gilchristella aestuaria*	2	10293	56.79	18.4	14.9	3.0-36.0	Pr,Fl,Po,Ju	+
Gobiidae	*Psammogobius knysnaensis*		26	0.11	<0.1	7.2	6.2-12.0	Po	
	Oligolepis acutipennis		6	0.03	<0.1	16.9	9.7-21.0	Po,Ju	+
	Redigobius sp.	19	84	0.38	0.1	6.3	3.5-9.0	Po	+
	Taenioides jacksoni	8	509	2.28	1.1	14.1	6.5-52.0	Po,Ju	
Eleotridae	*Eleotris fusca*		31	0.10	<0.1	19.4	11.0-22.0	Po	+
	Eleotrid 1		2	0.01	<0.1	10.2	10.0-10.3	Po	
	Eleotrid 2	14	131	0.57	0.2	13.2	11.0-19.0	Po	
	Eleotrid 3		5	0.02	<0.1	11.3	10.5-12.5	Po	
Marine spawners dependent on estuaries									
Elopidae	*Elops machnata*	7	555	2.64	0.9	32.1	19.0-37.0	Le	+
Engraulidae	*Thryssa vitrirostris*	5	831	3.70	1.2	19.9	11.0-42.0	Po,Ju	+
Teraponidae	*Terapon jarbua*	16	96	0.46	0.2	11.2	9.5-15.0	Po	+
Haemulidae	*Pomadasys commersonnii*		65	0.30	0.1	10.4	8.0-12.5	Po	+
Sparidae	*Acanthopagrus berda*								
	Monodactylus argenteus		13	0.06	<0.1	5.8	4.5-7.2	Fl,Po	+
	Rhabdosargus holubi	11	155	0.79	0.3	10.2	6.0-12.2	Po	+
	Rhabdosargus sarba		27	0.05	<0.1	10.3	8.0-12.0	Po	+
PARTIALLY ESTUARINE-DEPENDENT									
Catadromous									
Megalopidae	*Megalops cyprinoides*	17	103	0.46	0.2	25.7	17.4-31.0	Le	+
Freshwater and estuarine spawner									
	Glossogobius callidus	1	32585	215.26	65.1	6.7	3.0-40.0	Pr,Fl,Po,Ju	+

cont.

Table 6.1 cont.

Estuarine and marine spawners									
Chanidae	*Chanos chanos*		36	5.5	0.1	12.5	10.0-14.5	Po	+
Syngnathidae	*Hippichthys heptagonus*	18	100	0.42	<0.1	23.4	10.0-88.0	Po	+
Ambassidae	*Ambassis gymnocephalus*		1	<0.01	<0.1	48.0	48.0	Ju	+
	Ambassis sp.	10	303	1.69	0.5	6.2	4.0-12.0	Po	+
Gobiidae	*Callogobius* sp.		2	0.01	<0.1	16.0	14.0-18.0	Po,Ju	
	Croilia mossambica	3	2815	13.11	4.3	10.4	9.0-14.0	Po	+
	Gobiid 2		73	0.26	0.1	14.7	8.2-16.0	Po	+?
	Oxyurichthys opthalmonema		10	0.12	<0.1	21.7	21.0-41.5	Ju	
	Taenioides esquivel	4	651	3.93	1.4	10.2	6.5-12.0	Po	+
	Trypauchen microcephalus		17	0.08	<0.1	20.8	15.2-26.0	Ju	+
Marine spawners with juveniles abundant in estuaries									
Gerreidae	*Gerres* sp.1		6	0.03	<0.1	11.5	8.5-18.0	Po	+
Mugilidae	Mugilid spp.	10	0.08	<0.1	12.8	5.0-23.5	Po,Ju	+	
Soleidae	*Solea bleekeri*	9	492	2.00	0.7	7.4	3.8-27.0	Po,Ju	+
Marine spawners with juveniles at sea and in estuaries									
Engraulidae	*Stolephorus holodon*	6	630	2.83	0.9	20.2	6.5-46.0	Fl,Po,Ju	+
Chanidae	*Chanos chanos*		36	0.22	0.1	12.5	10.0-14.5	Po	+
Platycephalidae	*Platycephalus indicus*		3	0.01	<0.1	7.5	6.0-9.0	Fl,Po	+
Haemulidae	*Pomadasys kaakan*		14	1.6	<0.1	13.3	8.0-20.0	Po	+
Sillaginidae	*Sillago sihima*		13	0.04	<0.1	13.7	8.5-16.0	Po	+
Sciaenidae	*Johnius dussumieri*	13	166	0.74	0.2	12.3	5.0-41.0	Fl,Po,Ju	+
Leiognathidae	*Leiognathus equula*	12	203	0.76	0.3	12.8	5.2-27.0	Po,Ju	+
	Hemiramphus far		35	0.19	0.1	7.6	6.0-12.8	Po	+
	Pomadasys kaakan		14	0.07	<0.1	13.3	8.0-20.0	Po	+
	Hilsa kelee		3	0.01	<0.1	28.5	29.0-23.0	Ju	+
	Sphyraena jello		1	<0.01	<0.1	26.0	26.0	Ju	+
ESTUARINE-INDEPENDENT									
Freshwater									
Gobiidae	*Silhouettea sibayi*		42	0.14	<0.1	13.5	11.0-19.0	Po,Ju	
Reef and shore taxa									
Muraenidae	*Thrysoidea macrura*		31	0.11	<0.1	86.7	19.0-100.0	Le	+?
	Muraenid 2		1	0.1	<0.1	87.0	87.0	Le	
Ophichthidae	*Bascanichthys kirkii*		1	0.01	<0.1	62.0	62.0	Le	
	Ophichthus sp.1		20	0.11	<0.1	81.1	79.0-101.0	Le	+?
	Opichthid 1		4	0.01	<0.1	80.0	59.0-89.0	Le	
Muraenesocidae	*Muraenosox bagio*		13	0.06	<0.1	78.5	73.0-85.0	Le	+

cont.

Table 6.1 cont.

Clupeidae	*Herklotsichthys quadrimaculatus*		36	0.15	<0.1	15.5	11.0-24.0	Po,Ju	
Engraulidae	*Thryssa setirostris*		4	0.02	<0.1	29.3	30.0-31.0	Ju	+
Bregmacerotidae	*Bregmaceros atlanticus*		2	0.01	<0.1	10.5	10.5	Po	
Gobiesocidae	Gobiesocid 1		3	0.01	<0.1	6.0	6.0	Pr	
	Lepadichthys sp.1		6	0.03	<0.1	4.3	3.0-5.4	Pr	
Notocheiridae	*Iso natalensis*		6	0.02	<0.1	7.0	5.5-7.8	Pr	
Belonidae	*Strongylura leiura*		1	<0.01	<0.1	8.0	8.0	Po	+
Scorpaenidae	*Sebastapistes strongia*		3	0.01	<0.1	9.0	8.0	Po	
	Scorpaenid		1	0.1	<0.1	4.0	4.0	Fl	
Triglidae	Triglid		1	0.1	<0.1	6.0	6.0	Fl	
Serranidae	*Epinephelus* sp.1		2	0.01	<0.1	14.0	13.0-15.0	Po	+?
Haemulidae	*Pomadasys olivaceum*		33	0.15	<0.1	13.3	12.0-15.0	Po	+
Pempheridae	*Pempheris* sp.1		1	0.01	<0.1	5.5	5.5	Po	
Labridae	Labrid 4		1	<0.01	<0.1	7.0	7.0	Po	
Scaridae	*Scarussp.1*		2	0.01	<0.1	8.3	7.5-9.0	Po	+
Blenniidae	*Omobranchus banditus*		8	0.04	<0.1	13.5	4.0-27.0	Pr,Po,Ju	+
	Blenniid 1		6	0.03	<0.1	10.1	3.0-18.0	Pr,Fl,Po,Ju	
	Blenniid 2		1	<0.01	<0.1	11.0	11.0	Po	
Tripterygiidae	Tripterygiid 1		86	0.23	0.1	5.9	3.5-9.5	Pr,Fl,Po	
	Enneapterygius clarkae		1	<0.01	<0.1	13.0	13.0	Po	
Gobiidae	Gobiid 3		7	0.02	<0.1	8.0	7.5-8.5	Po	
	Gobiid 4	15	101	0.53	0.2	12.3	9.0-15.0	Po	+?
	Gobiid 5		1	<0.01	<0.1	12.5	12.5	Po	
	Gobiid 6		3	0.02	<0.1	6.6	6.0-7.2	Po	
Trichiuridae	Trichiurid 1		1	0.1	<0.1	18.0	18.0	Po	
Siganidae	*Siganus sutor*		2	0.01	<0.1	22.6	22.6	Ju	
Scombridae	Scombrid 2		3	0.01	<0.1	3.0	3.7-4.0	Pr	
	Scombrid 1		1	<0.01	<0.1	3.4	3.4	Pr	
Cynoglossidae	*Cynoglossus* sp.1		1	<0.01	<0.1	13.8	13.8	Po	
Ostraciidae	Ostraciid 1		1	0.01	<0.1	7.0	7.0	Po	
Tetraodontidae	*Arothron immaculatus*	20	79	0.34	0.1	9.8	7.5-13.0	Po	+
Myctophidae	*Benthosema pterotum*		8	0.04	<0.1	6.2	4.5-8.0	Pr,Po	
	Hygophum hygomii		3	0.01	<0.1	5.4	4.8-6	Pr	
	Hygophum proximum		1	<0.01	<0.1	4.0	4.0	Pr	
	Lampanyctus alatus		16	0.06	<0.1	3.8	3.0-7.2	Pr,Fl,Po	
	Scopelopsis multipunctatus		10	0.04	<0.1	8.5	4.0-14.0	Pr,Fl,Po	

Total number = 51690 51701.1
Total number of taxa = 85
Total number families = 44

^ Wallace (1975a,b); Wallace and van der Elst (1975); Whitfield (1980).

Multiple regression analyses for each estuarine-association group showed that different combinations of environmental variables were important in accounting for the variability in larval densities, and that it is species-specific within each group (Table 6.2). Turbidity and salinity accounted for 45% of the variation in larval densities in the estuarine-dependent group where densities were higher at higher turbidities and lower salinities ($P < 0.001$). The negative correlation with salinity was highly significant for two abundant species which spawn in estuaries and are dependent on them, *G.aestuaria* and *T.jacksoni* ($P < 0.001$). Conversely, densities of two other abundant species which are marine spawners but are dependent on estuaries (*T.vitrirostris* and *R.holubi*) changed in relation to temperature, turbidity and current velocity. Larval densities of *G.callidus* were significantly higher at higher turbidities ($P < 0.001$) and at lower current velocities ($P < 0.001$) and salinities ($P < 0.05$). Although, salinity, temperature and current velocity only accounted for 8% of the variation in larval densities of estuarine-independent taxa, this was significant ($P < 0.001$) (Table 6.2).

Table 6.2. Stepwise regression statistics of larval fish densities versus environmental variables (cu, current; sa, salinity; te, temperature; tu, turbidity) for each estuarine-association group and the most abundant species in each group, in St Lucia Estuary. (adj; adjusted R^2; coefficient of determination; R, correlation coefficient; F, F statistic)

Estuarine-association group	adjR^2	R	F	significant variables
All taxa	0.36	0.60	92.15***	tu***; te**
Estuarine-dependent	0.45	0.67	70.71***	tu***; -sa***
Gilchristella aestuaria	0.42	0.65	43.55***	tu***; -cu**; -sa*
Taenioides jacksoni	0.09	0.30	8.06***	-sa***; te*
Thryssa vitrirostris	0.02	0.15	4.87*	te*
Rhabdosargus holubi	0.08	0.29	8.72***	tu**; cu*
Partially estuarine-dependent	0.29	0.54	31.28***	tu***; te**
Glossogobius callidus	0.43	0.66	43.64***	tu***; te***; -sa***
Croilia mossambica	0.12	0.34	12.63***	tu***; sa*
Ambassis sp.	0.02	0.15	4.98*	cu*
Stolephorus holodon	0.12	0.35	12.93***	tu***; sa***
Estuarine-independent	0.09	0.30	9.0***	sa**; te*; cu*

P<0.05; **P<0.01;***P<0.001

6.2.3 Estuarine-Association

In terms of density, larvae of fish species partially dependent on estuaries comprised 74.1% of the total catch (Figure 6.3). Approximately 25% of the total catch were larvae of estuarine-dependent species. Of the 85 taxa recorded at the sample site in the St Lucia Estuary, 17 taxa (20% of the total) were estuarine-dependent species. Included in this group were a few glass eel stage freshwater eel (*A.mossambica*; Figure 6.3). The dominance of larvae in the partially estuarine-dependent group was predominantly from an abundance of larvae of the goby *C.mossambica.* Larvae of 38 taxa were reef- and shelf-associated species (see Table 6.1) and larvae of five myctophid species account for the oceanic taxa (Figure 6.3).

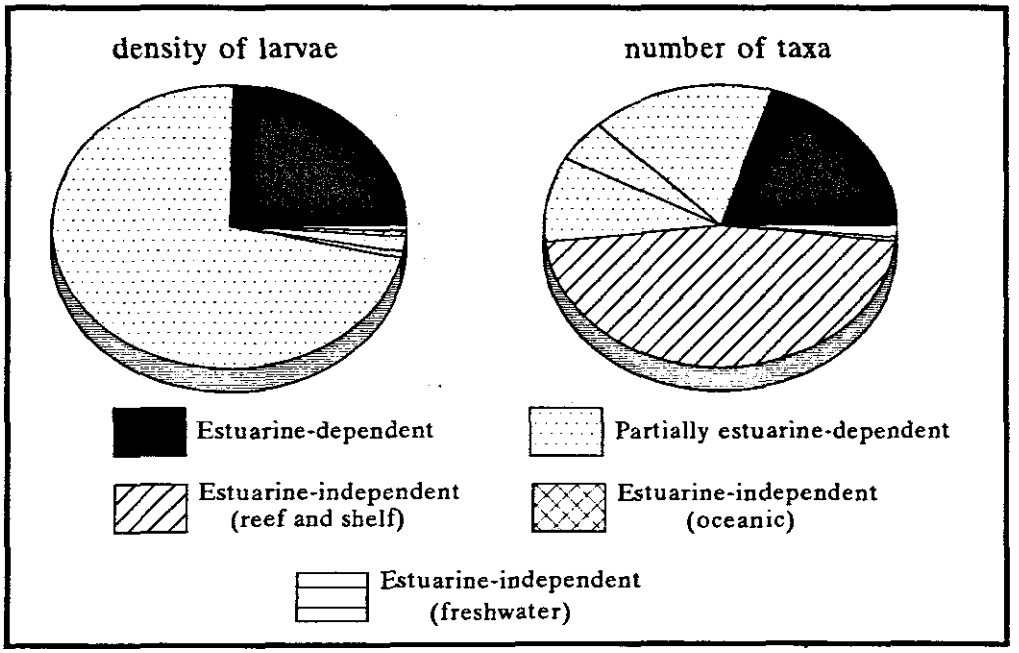


Figure 6.3. Percentage contribution of the estuarine-association groups, in terms of density of larvae and number of taxa, for all taxa sampled in the study.

6.2.4 Seasonal Trends in Larval Fish Density

No significant differences in larval densities between top and bottom samples were found for all taxa ($F = 0.16$; $P = 0.69$), therefore, top and bottom values were combined. Larval densities of all taxa together were highest from late spring (November 1987, 1033 larvae per 100 m^3) to early autumn (April 1988, 556 larvae per 100 m^3), except in February when the density dropped to 31 larvae per 100 m^3 (Figure 6.4A). Lowest densities occurred during June 1988 (15 larvae per 100 m^3) and were low throughout the winter months.

Larval densities in each estuarine-association group followed different monthly trends since for each sampling period different taxa dominated the catch (Figure 6.4B, C, and D, and Figure 6.5). Top and bottom densities for each group were also not significantly different and so were combined ($P > 0.05$). Estuarine-dependent taxa were most abundant in January, March, April and September (Figure 6.4B) due to an abundance of larval *G.aestuaria* in those months (Figure 6.5). Partially estuarine-dependent taxa followed the same trend as all taxa together (Figure 6.4C) since the most abundant species, *G.callidus*, falls into this group. *G.callidus* was particularly abundant from November 1987 to the beginning of May 1988 (late spring and early autumn). Note that larvae of the flatfish *S.bleekeri* were abundant in early and late May 1988 (Figure 6.5). Larval densities of taxa in the estuarine-independent group were considerably lower than the other two estuarine-association groups with the mean density being highest in March 1988 (Figure 6.4D). Since densities of estuarine-independent taxa were so low, no particular marine straggler species dominated the catch in any of the months (Figure 6.5).

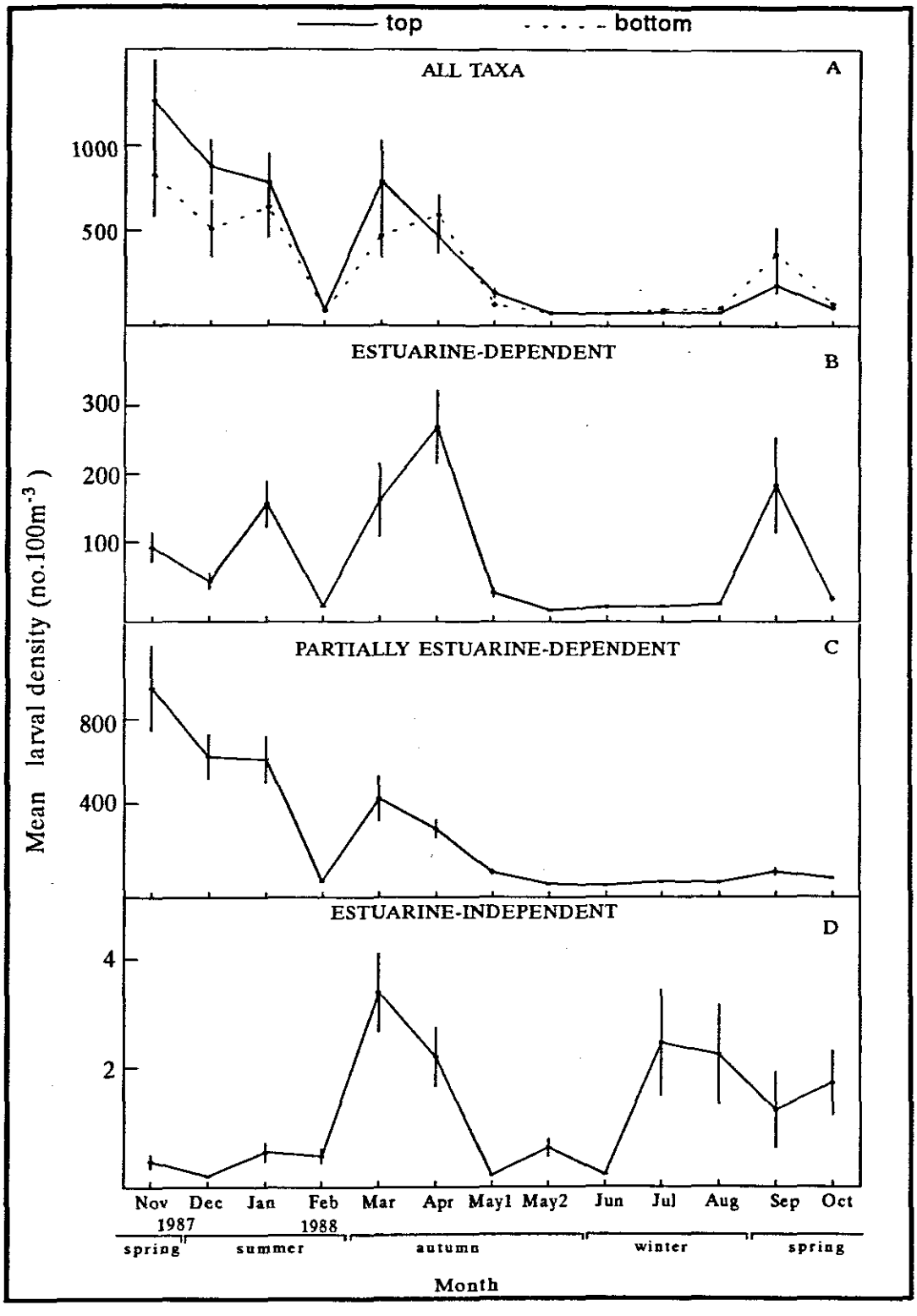


Figure 6.4. Mean monthly variations in larval densities (± 1SE) for all taxa together (A, top and bottom), estuarine-dependent taxa (B), partially estuarine-dependent taxa (C) and estuarine-independent taxa (D). (for B, C, and D top and bottom values are combined)

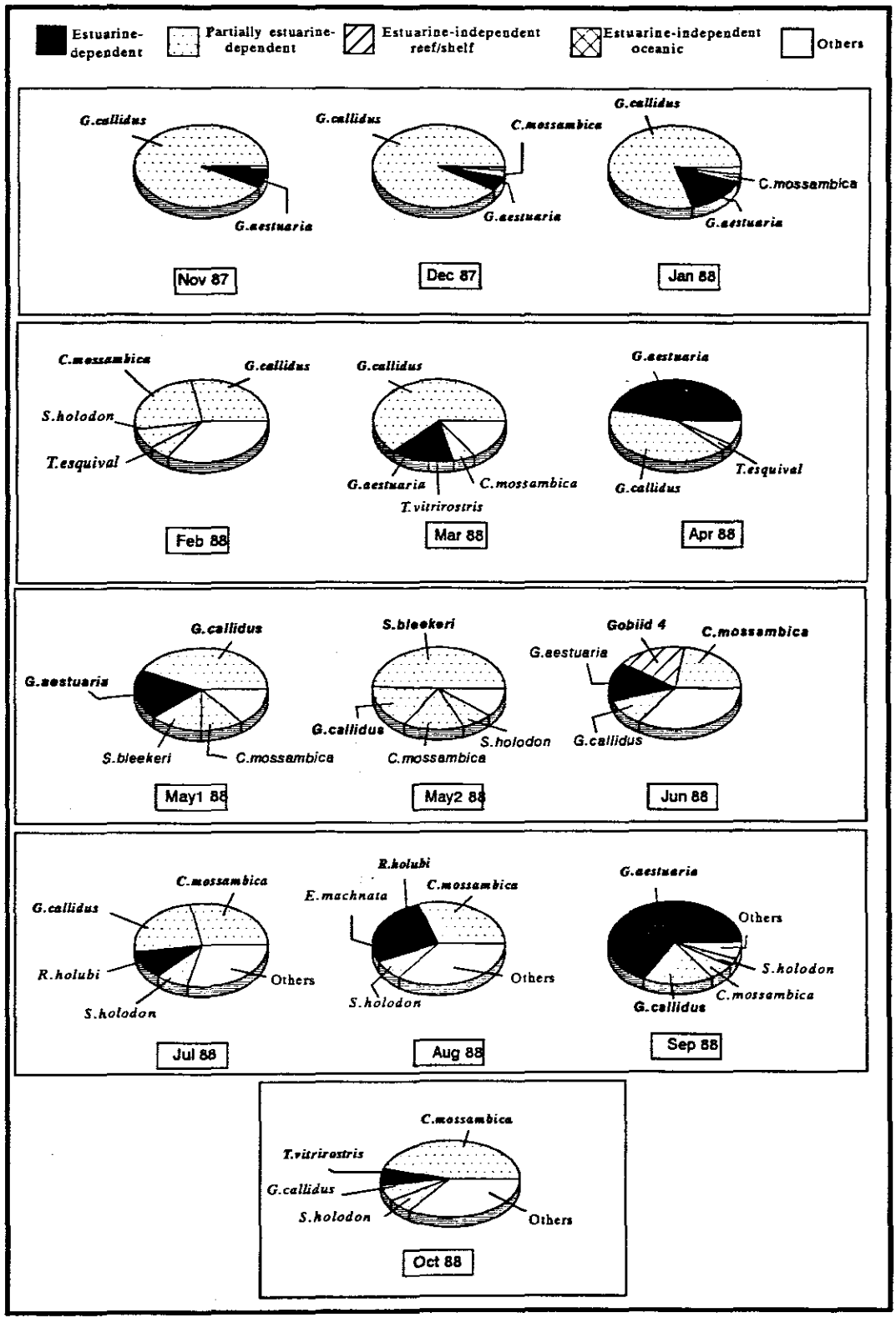


Figure 6.5. Percentage contribution of the most abundant species in the total catch sampled each month in the St Lucia Estuary

6.2.5 Developmental Stages

Over 25% of developmental larval stages of estuarine-dependent species were preflexion and flexion (young larvae) with glass eel stages comprising 5.7% of this group (Figure 6.6). Juveniles of estuarine residents, *G.aestuaria* and two gobiid species, accounted for the juvenile component of this group. Partially estuarine-dependent taxa were predominantly postflexion larvae (96.5%) and estuarine-independent taxa were present at all stages of development. The leptocephali larvae were due to the presence of *E.machnata*, marine eel species an d *M.cyprinoides*.

Postflexion larvae predominated in all months, except in September when preflexion larval stages were abundant (Figure 6.7). In the spring month of September, 67% of the total catch was dominated by preflexion stages of *G.aestuaria*.

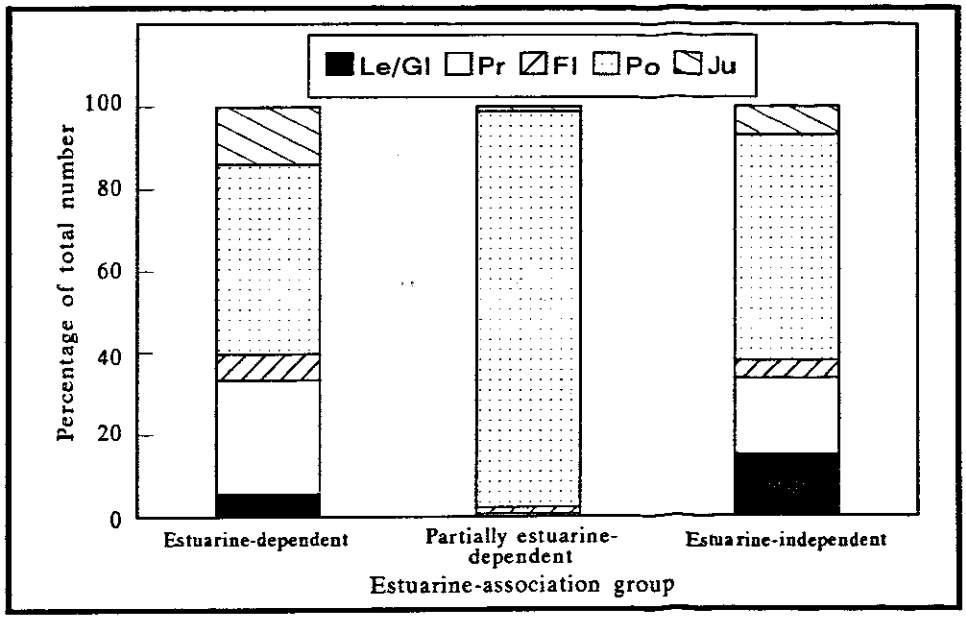


Figure 6.6. Percentage composition of the different developmental stages of all larvae for each estuarine-association category. Gl, glass eel; Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile.

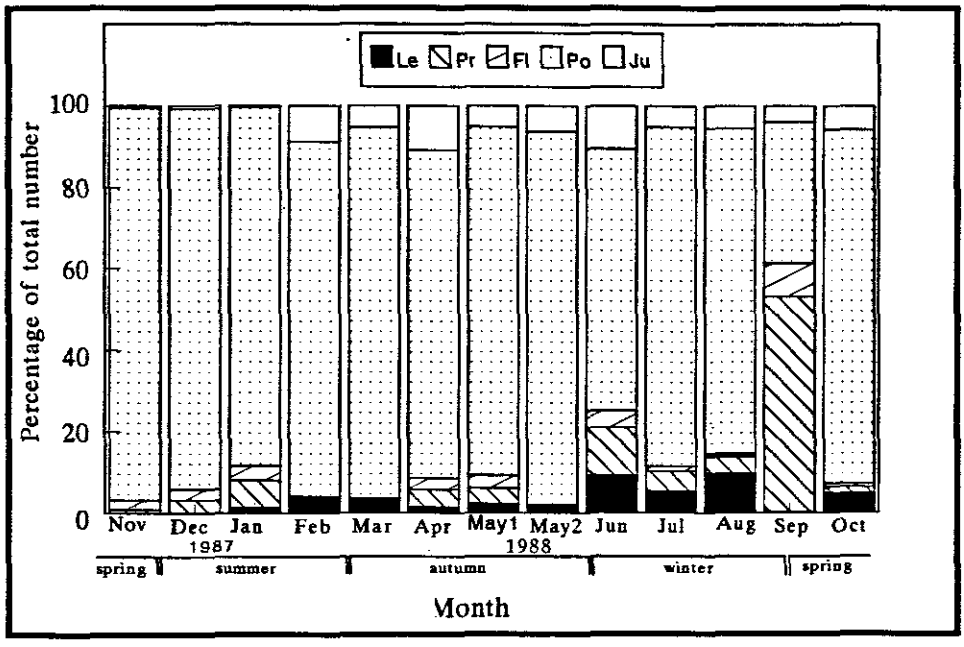


Figure 6.7. Monthly percentage composition of developmental stages of all larvae sampled in the study. Gl, glass eel; Le, leptocephali; Ys, yolk sac; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile.

6.3. DISCUSSION

6.3.1. Composition of the Larval Fish Assemblage

The larval fish in St Lucia are characterised by a few dominant species that are present in large numbers. This is a common characteristic of both southern and northern hemisphere estuaries (Melville-Smith and Baird 1980; Jenkins 1986; Roper 1986; Whitfield 1989; de la Fontaine 1990; Gaughan *et al.* 1990; Harrison and Whitfield 1990; Neira *et al.* 1992; Tzeng and Wang 1992; Yoklavich *et al.* 1992). In particular, the Gobiidae and/or Clupeidae make up the major contribution (Melville-Smith and Baird 1980; Jenkins 1986; Roper 1986; Whitfield 1989a; Gaughan *et al.* 1990; Harrison and Whitfield 1990; Neira *et al.* 1992; Yoklavich *et al.* 1992), with the species in these two families ranking first to fourth in the present study. The species of Elopidae and Soleidae, which ranked seventh and ninth in terms of abundance, were represented by only one species (Table 6.1). The presence of only one species in the dominant families has also been noted by Neira *et al.* (1992) in temperate south-west Australia.

Species diversity of fish fauna in south-east African estuaries varies according to latitude and the individual characteristics of each estuary (Day *et al.* 1981). The number of larval taxa recorded in the subtropical St Lucia Estuary was much higher than those recorded from the temperate estuaries in the south-eastern Cape (Table 6.3). The juvenile and adult fish fauna of KwaZulu-Natal estuaries is dominated by tropical species (Blaber 1985) which accounts for the large number of larval taxa recorded in the present study. The nature of the estuarine system affects the fish faunal diversity (Blaber 1985) with the open/closed condition of an estuary probably being the major determinant of fish species diversity and abundance in southern Africa (Whitfield and Kok 1992). Bennett (1989a) has shown that the differences in the fish species composition of permanently open, seasonally open and closed estuaries are related to the differences in the duration of the connection between the estuaries and the sea.

Not only is larval species diversity different at different latitudes but so is species composition. For example, larval stages of the most abundant gobiid species caught in the temperate south-eastern Cape estuaries were *Psammogobius knysnaensis* and *Caffrogobius multifasciatus* (Melville-Smith and Baird 1980; Melville-Smith 1981;

Beckley 1985a; Whitfield 1989b; Harrison and Whitfield 1990). In contrast, the most abundant goby in the subtropical St Lucia Estuary in this study, was *G.callidus*, contributing 65% of the total (see Table 6.1). Additionally, in the earlier study of Martin *et al.* (1992) the most abundant gobies in the St Lucia Estuary were *C.mossambica*, *G.callidus* and *Gobius acutipennis*.

Table 6.3. Number of larval fish taxa in South African estuaries.

Estuary	Latitude	Region	Estuary type	No. taxa	Source
Kromme	34°08'S	temperate, Western Cape	small, permanently open	12	Melville-Smith (1981)
Swartvlei	34°00'S	temperate, Western Cape	small, seasonally open	9	Whitfield (1989a)
Swartkops	33°51'S	temperate, Eastern Cape	small, seasonally open	19	Melville-Smith and Baird (1980)
Sundays	32°42'S	temperate, Eastern Cape	medium, permanently oper	19	Harrison and Whitfield (1990)
St Lucia	28°23'S	subtropical, KwaZulu-Natal	large, permanently open	85	present study

The presence of oceanic taxa such as myctophids is probably a result of the shoreward intrusion of Agulhas Current surface water which is consistently recorded along the KwaZulu-Natal coast (Beckley and van Ballegooyen 1992). Miskiewicz (1987) similarly recorded the occurrence of oceanic taxa in Lake Macquarie, south-east Australia, and attributed this to pulses of oceanic water into the estuary.

The St Lucia sampling station was situated 4 km from the mouth and so can be considered as lower reaches of the estuary since tidal effects penetrate for 14 km (Wright and Mason 1990). Of the 133 fish species which are associated with estuaries in subtropical southern Africa, 70% have a relatively strong association with these estuaries (categories I and II, Whitfield 1994a). The larval taxa sampled in the present study had a smaller proportion of taxa from these two categories (51%) with 46% being categorised as marine straggler species not dependent on estuaries. The greater proportion of species from the marine stragglers in larval stages is because of the presence of a higher number of vagrants that may be transported passively into the estuary.

A large proportion of estuarine-dependent and partially dependent larval taxa recorded in the present study (72% and 74%, respectively) have also been recorded as juveniles and/or adults in St Lucia (Table 6.1, last column). Alternatively from the aspect of spawning strategy, 41% of estuarine spawners and 95% of marine spawners dependent on estuaries to some degree were recorded as larvae but have also been recorded as juveniles and/or adults in St Lucia (Table 6.1). Although only one station was sampled in the present study, it appears that the majority of the marine fish species utilizing St Lucia are passing at the station sampled and are entering the system at the postflexion larval stage. Additional studies are needed to examine the spatial distribution of larval abundance in the whole St Lucia system.

6.3.2 Larval Fish Abundance in Relation to Environmental Factors

The St Lucia Estuary mouth is flood tide dominated with a maximum current velocity on the bottom of 0.72 ms^{-1} on the spring flood tide, compared to 0.34 ms^{-1} on the spring ebb tide (Wright and Mason 1990). This suggests a net upstream movement of bottom water which would facilitate larval transport into the St Lucia system. The present study only sampled on the spring flood tide and also recorded a maximum current velocity of

0.70 ms^{-1}. A number of studies have shown that fish larvae are often present in large numbers near the bottom of estuaries (Weinstein *et al.* 1980; Norcross and Shaw 1984; Steffe 1990) or near the banks of the estuary mouth channel (Beckley 1985a) to avoid being flushed out with the ebb tide. In the estuaries of the eastern Cape the larvae of *G.aestuaria* (7-13 mm) have been reported to use tidal currents to maintain their position in an estuary with larvae being more abundant in the bottom waters (Melville-Smith *et al.* 1981; Harrison and Whitfield 1990). In the present study, no significant differences in larval densities between top and bottom samples were detected ($P > 0.05$, for all taxa together and individual dominant species). This was probably due to the fact that only one station was sampled and only on flood tides. A more detailed study is required which specifically investigates this phenomenon. However, current velocity did have a significant negative relationship with densities of larval *G.callidus* ($P < 0.001$) and that there were higher densities in bottom samples, although this was not significant (ANOVA, $P = 0.059$). The negative relationship of lower densities at higher current velocities suggests that *G.callidus* is avoiding the current. Larval denisities of the estuarine independent group was also related to current velocity, but with higher densities at higher current velocities ($P < 0.05$) which is what one would expect since these larvae are stragglers being washed passively into the estuary.

South African estuaries are highly variable environments where fluctuations in physical conditions such as salinity, temperature and turbidity occur regularly and hence affect the breeding of resident fish species (Day *et al.* 1981). The St Lucia Estuary is renowned for large salinity and turbidity fluctuations between < 2 - 114 ‰ and 6 - 238 NTU (Cyrus 1988; Whitfield 1990), respectively. The study of Cyrus and Blaber (1987b) showed that the distribution and abundance of the juvenile marine fish in the St Lucia system are correlated with water temperature and turbidity. In the present study, overall larval densities were also positively correlated with the latter two variables. In addition to turbidity and temperature, salinity and current velocity also had significant correlation's with larval densities of estuarine-associated taxa (Table 6.2). Whitfield (1994c) suggested it is unlikely that one physical factor alone is responsible for eliciting recruitment migrations into estuaries and that it depends on estuary type and amount of riverine input into the system.

The response of larval densities to environmental variables has been shown to be species-specific (Tzeng and Wang 1992). This is illustrated by the present study where overall larval densities were correlated to a different set of variables than were individual species. For example, salinity was not a significant variable when all taxa are in the multiple regression model but densities of the most dominant species (*G.callidus* and *G.aestuaria*) had significantly higher densities at lower salinities. Tzeng and Wang (1992) similarly found a negative correlation between abundance of the dominant estuarine-dependent species and salinity. Neira *et al.* (1992) found that the most abundant larvae in the Swan Estuary, Australia, belong to the estuarine spawner category and occurred predominantly in the upper, less saline reaches of the estuary.

The effects of salinity on larval fish abundance in the St Lucia Estuary is clearly illustrated in the study of Martin *et al.* (1992). Their study found that in the two years before the floods of Cyclone Domoina (January 1984), salinities in the estuary ranged from 28 ‰ to 36 ‰ and the most abundant species were *C.mossambica* which breeds in estuaries and at sea and *S.holodon* which breeds at sea. In the months following the flood, salinities decreased sharply, to as low as 6 ‰, with the abundance of the estuarine spawner *G.aestuaria* increasing sharply from 2% of the catch before the flood to 34% after the flood. Whitfield (1994c) found that the most important factor associated with abundance of early life stages of fish in the eastern Cape estuaries is the axial salinity gradient. From the results of the present study, it appears that salinity is also an important environmental variable in St Lucia Estuary, although turbidity is more important (Table 6.2). Turbidity is also one of the most important factors affecting fish distribution in estuaries (Blaber and Blaber 1980) and, in particular, the St Lucia system where Cyrus (1984) did extensive studies on the effects of turbidity on the juvenile and adult fish in this system. Turbidity was the most significant environmental variable correlated to larval fish densities (Table 6.2) with higher densities at higher turbidities. Martin *et al.* (1992) also found that elevated turbidities associated with flooding clearly contributed to increased recruitment of the fish larvae and juveniles in the St Lucia Estuary (particularly the marine migrants). Marais (1988) obtained positive correlation's between fish abundance and turbidities in 14 estuaries along the south and south-east coast of South Africa. Turbid water conditions are advantageous to larval Pacific

herring (*Clupea harengus*), an estuarine spawner, due to enhanced feeding abilities and reduced predation under turbid water conditions (Boehlert and Morgan 1985).

6.3.3 Seasonal Trends in Larval Fish Abundance

Larval densities in St Lucia followed a seasonal trend with peak abundances occurring from spring to early autumn and declining to a minimum in late autumn and winter. This seasonal pattern parallels the situation occurring in many other estuaries (Able 1978; Melville-Smith and Baird 1980; Melville-Smith 1981; de la Fontaine *et al.* 1984; Jenkins 1986; Roper 1986; Miskiewicz 1987; Whitfield 1989a; Harrison and Whitfield 1990; Warlen and Burke 1990; Gaughan *et al.* 1990; Neira and Potter 1992; Neira *et al.* 1992; Tzeng and Wang 1992).

A number of studies have shown clearly that it is the physical conditions (temperature, salinity and turbidity) in an estuary which influence the monthly variation of occurrence of the different life-cycle categories of larval and juvenile fish recruiting into estuaries (Loneragan and Potter 1990; Martin *et al.* 1992; Neira *et al.* 1992; Whitfield 1994a). Loneragan and Potter (1990) showed that the species composition of fish in the Swan Estuary changed seasonally, particularly in the upper estuary where salinities were reduced in winter and spring due to increased freshwater input and estuarine species dominated. Freshwater inflow is the key factor regulating both the structure and functioning of the St Lucia estuarine system (Taylor 1982) where salinity, turbidity and temperature gradients can change over very short periods of time (Cyrus and Blaber 1987b). In the months following a cyclone in January 1984, the reduced salinities and increased turbidities in the sea off the mouth of the St Lucia Estuary contributed to short-term changes in recruitment densities of most of the fish species, particularly the marine migrants (Martin *et al.* 1992). The study of Whitfield (1994c) indicated that the axial salinity gradient in eastern Cape estuaries is the single most important factor associated with abundance of larval and juvenile marine fishes. For the present study of St Lucia, the larval fish densities were most influenced by turbidity, however, salinity, temperature and current velocity were also important variables for certain estuarine-dependent groups and individual species. In addition, the relationship

of larval densities with turbidity was on a seasonal basis since the monthly trend in larval abundance coincided with the monthly trend in turbidity (see Figures. 6.1 and 6.4).

Recruitment of most juvenile fish species into temperate southern Cape estuaries reaches a peak in summer (Whitfield and Kok 1992) and subtropical Natal estuaries in late winter and spring (Wallace 1975a,b) with many of these species having a protracted recruitment period (Wallace 1975a; Whitfield and Kok 1992). The present study indicates that recruitment of larval stages of marine spawner species into St Lucia Estuary occurred mainly in spring, summer and autumn.

6.3.4 Developmental Stages of Larvae and Recruitment Strategies

In general, marine species that recruit into estuaries from offshore do so at advanced developmental stages (Kendall *et al.* 1984; Boehlert and Mundy 1988). This seems to be the case for both subtropical and temperate estuaries world-wide where a predominance of old larvae (postflexion) and juveniles recruit into estuarine nursery areas at certain times of the year (Melville-Smith and Baird 1980; Melville-Smith 1981; Whitfield 1989a; Harrison and Whitfield 1990; Tzeng and Wang 1992; Warlen 1994; Niera and Potter 1994). The predominance of postflexion larval stages in the subtropical St Lucia estuary for all estuarine-association categories and throughout the year (Figure 6.7) follows this pattern.

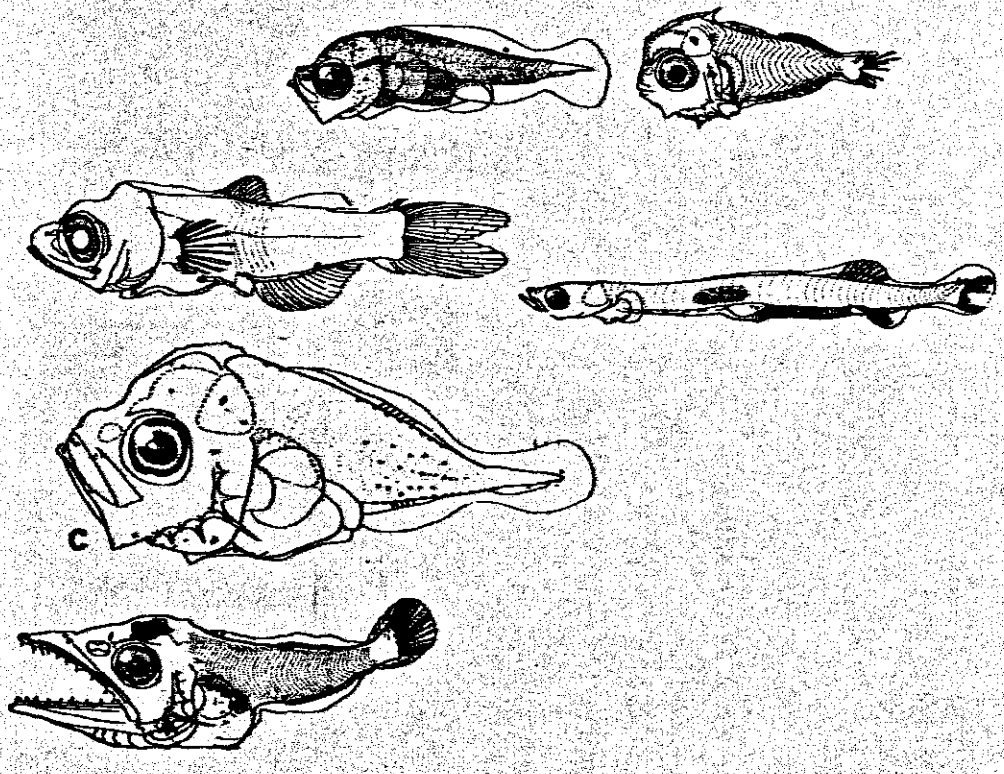
The absence of larvae of the marine species *A.hololepidotus* (kob), which are abundant as juveniles and/or adults in the St Lucia Estuary (Wallace and van der Elst 1975), implies that this species usually enters the St Lucia Estuary as juveniles or adults. The study by Wallace and van der Elst (1975) showed that recruitment of *A.hololepidotus* into the St Lucia Estuary starts at 50 mm but is most intensive between 80-150 mm. Other authors have similarly found that although certain species, particularly in the family Mugilidae, are dominant as juveniles and adults in the estuary, no larvae were sampled in these estuaries (Melville-Smith and Baird 1980; Gaughan *et al.* 1990; Neira and Potter 1992; Neira *et al.* 1992) indicating recruitment into the estuary at a larger size range. Whitfield (1994c) compared recruitment of fish larvae and juveniles into three Eastern Cape estuaries with differing freshwater input and found that marine migrants (sparids and mugilids) recruited to the Great Fish Estuary at a smaller

size range than to the Sundays and Kariega estuaries. He attributed this to two possible reasons: the lower salinities associated with the Great Fish Estuary or closer proximity to spawning grounds. Miskiewicz (1986) also showed that the major factor causing the difference in the average length at which three sparid larvae enter Lake Macquarie Estuary in New South Wales is the proximity of the spawning grounds. In the St Lucia Estuary, the majority of larvae of the marine spawners with some degree of estuarine dependence were postflexion. This indicates that their spawning grounds are not in the immediate vicinity of the estuary mouth and that they spend some time at sea in shelf waters or in the surf zone adjacent to the estuary (see Chapters 8 and 9) until they have developed fins (i.e. reached postflexion stage) and actively migrate into the estuary.

The relationship between the proximity of spawning grounds and size range of larvae in estuaries is clearly seen for the estuarine spawner category: For example, in the St Lucia Estuary there was an abundance of young larvae (preflexion and flexion stages) in September (Figure 6.7) which were predominantly larval stages of the estuarine spawner *G.aestuaria*. The predominance of preflexion larvae is also due to marine straggler species being washed passively into the estuary on flood tides.

CHAPTER 7

A Comparison of the Larval Fish Assemblages in Three Large Estuarine Systems



7. COMPARISON OF THE LARVAL FISH ASSEMBLAGES IN THREE LARGE ESTUARINE SYSTEMS

7.1. Introduction

Estuaries are highly variable and unstable environments (Whitfield 1990) and the communities living in such environments theoretically would not reach an equilibrium state. If biotic factors, such as interspecific competition, are prevalent in a community an equilibrium state could be reached (i.e. concept of harsher or less stable habitats contain fewer species). Sanders (1968) hypothesised that communities are either physically or biologically controlled. Only certain organisms can survive in harsh or stressed environments and so these communities are physically controlled. Conversely, where physical conditions are benign, interspecific competition is important and so a community is biologically controlled. Morais and Morais (1994) found that the larval and juvenile fish community in a tropical estuary in French Guiana was at a relative equilibrium but that annual variations in physical conditions affected recruitment and hence the composition of the assemblage.

Perturbations on estuarine systems increases environmental stress upon the organisms living in these systems and subsequently decreases the stability of a system, which reduces their value as a nursery habitat. Canalization, dredging, pollution, siltation and recreational activities have been shown to dramatically reduce the diversity of the fish fauna in an estuarine system (Day *et al.* 1955; Begg 1978; Felley 1987; Haedrich 1983; Cooper *et al.* 1995). Three of the largest estuarine systems on the KwaZulu-Natal coast of South Africa have changed drastically from their original state: Durban and Richards Bay now function as important harbours (Guastella 1994) with major developments existing on their perimeters, and the St Lucia estuarine system suffers from very high siltation rates due to poor farming techniques in the catchment, with additional pressure from recreational activities (Taylor 1982; Wright and Mason 1990). The ichthyofauna in these estuarine systems is, presumably, impacted upon in one way or another and becomes stressed.

In assessing the larval fish assemblages in estuarine systems the majority of studies give basic descriptions of the species composition of the assemblage and analyse

patterns of abundance and seasonality. The analyses are generally descriptive with graphical representations of abundance patterns and simple or univariate statistical tests (ANOVAs and Regressions) applied to the data (e.g. Able 1978; Melville-Smith and Baird 1980; de la Fontaine *et al.* 1984; Jenkins 1986; Whitfield 1989a; Gaughan *et al.* 1990; Whitfield and Harrison 1990; Tzeng and Wang 1992). In addition to these methods, more recent studies have used multivariate techniques of classification/cluster analysis and multidimensional scaling (MDS) to gain better insight into how the assemblages are structured (Neira and Potter 1992; Neira *et al.* 1992; Neira and Potter 1994; Morais and Morais 1994). These latter studies describe how the larval fish communities are structured but little is known about why estuarine larval fish communities are structured in a particular pattern.

The relationship between biotic and abiotic measurements using classification and ordination have, however, been applied to juvenile and adult fish assemblages in a number of estuarine systems. Species groups tended to separate out on the basis of station and habitat type and/or season (Felley 1987; Robertson and Duke 1987; Bennett 1989a; Whitfield *et al.* 1989; Loneragan and Potter 1990; Neira *et al.* 1992; Potter *et al.* 1993; Blaber *et al.* 1994; Neira and Potter 1994; Pollard 1994). For example, it has been shown that juvenile and adult fish communities in tropical estuaries in northern Australia are associated with particular sets of physical conditions (Blaber *et al.* 1994).

Since community data is inherently multivariate (Clarke and Warwick 1994), analyses of data should incorporate a range of methods including both univariate and multivariate tests to obtain a complete picture of how and why a biotic community is structured. Univariate methods such as diversity indices provide a measure of the way in which the total number of individuals is divided up among the different species and is amenable to simple statistical tests. Multivariate techniques generally involve the classification (clustering) and ordination of community data which discriminates sites on the basis of their biotic composition and graphically shows community differences between groups of samples (James and McCulloch 1990; Clarke and Warwick 1994). There are other multivariate techniques, such as, principal components analysis (PCA) and multiple stepwise regressions, with certain limitations applying to all the techniques (James and McCulloch 1990). Studies which have employed multivariate analyses on larval and/or juvenile fish communities have used a variety of computer programs such

as TWINSPAN (Loneragan and Potter 1990; Potter *et al.* 1993), DECORANA (Felley 1987; Loneragan and Potter 1990; Pollard 1994), PATN (Neira and Potter 1992; Neira *et al.* 1992; Blaber *et al.* 1994; Neira and Potter 1994), PCA and CANOCA/ADDAD (Tzeng and Wang 1993; Morais and Morais 1994) and the methods described by Field *et al.* (1982) (Bennett 1989a; Whitfield *et al.* 1989). PRIMER (Plymouth Routines in Multivariate Ecological Research) has been developed recently by Clarke and Warwick (1994), specifically for multivariate analyses of marine communities, which is a further advance on Field *et al.* (1982). Species groups characteristic of particular estuarine habitats and environmental conditions have been recognised by all these techniques.

The larval fish assemblages in Durban Harbour, Richards Bay Harbour and St Lucia Estuary have been described in detail in Chapters 4, 5 and 6 using graphical and certain univariate and multivariate statistical techniques (ANOVAs and Stepwise Regressions). Results from these Chapters indicate that intercorrelations exist between the environmental factors measured with different combinations of factors accounting for the variability in larval densities of each estuarine-association group. This aim of this chapter is to compare the structures of the larval fish assemblages in the three estuarine systems and to relate this to the environmental factors which may be important in structuring those communities. A combination of univariate (diversity indices), distributional (dominance curves) and multivariate (classification and ordination) techniques is used since each method gives different information which aids in the interpretation of the data. The following questions are addressed:

- does each estuarine system have a different larval fish assemblage structure ?
- do groups of species separate out on the basis of their estuarine-association category?
- are these communities stable or at an equilibrium in an unstable environment ?
- do the physical conditions and environmental variables play an important part in structuring those communities ?
- what intercorrelations exist between abiotic factors and how does this influence assemblage structure ?

7.2. Analyses of Data

Larval fish density data from Durban Harbour, Richards Bay Harbour and the St Lucia Estuary were used in the analyses (Chapters 4, 5 and 6). To recap, densities of all species, from each estuarine system, were standardised to number of larvae per $100m^3$ (see section 3.2.2, Chapter 3). These data were then placed in a matrix with species as rows and samples as columns (212 species over 38 months - Appendix 6). If all samples taken each month at each site are used (229 for Durban Harbour; 208 for Richards Bay Harbour; and 312 for St Lucia Estuary i.e. total samples = 749) the matrix becomes too large to analyse. Therefore, the mean monthly densities of each species at each location were used as the samples. Using mean monthly values has the advantage of simplifying large data sets with little loss of information and identifying interrelations among variables (Morais and Morais 1994). For the environmental data matrix, mean monthly values of salinity, temperature and turbidity were used.

The software program used for all the analyses was PRIMER v3.1b (Plymouth Routines in Multivariate Ecological Research) devised by Clarke and Warwick (1994) in addition to following the methods of Field *et al.* (1982). The data were analysed according to a combination of univariate, graphical and multivariate analyses in the following way:

1.) Species diversity and evenness

Shannon-Wiener's Diversity Index: $H' = -\sum_i p_i (\log p_i)$

Pielou's Evenness Index: $J' = H'(\text{observed})/H'_{max}$

2) Graphical representation

Dominance curves (ordinary, partial and cumulative) - based on the ranking of species in decreasing order of their importance in terms of abundance. The ranked abundances are plotted against the logged species rank (logging the x-axis enables the distribution of commoner species to be better visualised. Partial dominance curves places more emphasis on the middle ranked species rather than

the highest. Cumulative or K-dominance curves are the ranked abundances plotted against log species rank where the most elevated curve has the lowest diversity.

Geometric abundance curves - percentage of species that are represented by 1 individual in geometric size class 1, 2-3 individuals in class 2 etc. (a x2 geometric size class). This plot may detect the effects of pollution stress - in an unpolluted (unstressed) situation there are many rare species and the curve is smooth with its mode well to the left, and in a polluted situation there are fewer rare species and more abundant species so the curve is more irregular.

3) Classification

Biotic data - hierarchical agglomerative clustering with group-averaging linking, based on the Bray-Curtis Similarity measure (ranked) was used to delineate groups with distinct community structure. Abundance values were root-root transformed for the analysis. The root-root transformation down-weights the more abundant species and is invariant to scale change (Field *et al.* 1982). Two types of classification analyses were done :

- by site using all species
- by species (inverse analysis) using only the top 20 ranked species from each site (see Tables 4.1, 5.1 and 5.1) i.e. total 41 dominant species. Indicator species at each site could then be identified using the program SIMPER which examines the contribution of individual species to the similarity measure used.

Abiotic data - environmental variables were log transformed [log10 (x + 1)], where necessary, to conform to normality. Hierarchical agglomerative clustering with group-averaging linking, based on the Normalised Euclidean Distance Dissimilarity measure (ranked) was used to delineate groups.

4) Ordination

Non-metric multidimensional scaling (MDS) was used where a stress level of <0.20 gives an adequate representation of the 2-dimentional MDS. At least 10 runs were undertaken to find the global minimum i.e. runs are done until two or more solutions with the same stress value is achieved.

5) BIO-ENV procedure

This relates the biotic to the abiotic factors by superimposing the environmental data on the biotic ordination i.e. links the community data to the environmental variables. The premise here is that if a suite of environmental variables is responsible for structuring the community, the abiotic ordination would be similar to the biotic groupings (Clarke and Warwick 1994). From the MDS plots one can determine which environmental variables may be influencing the community structure.

6) Statistical tests

For discrimination between sites one-way ANOVA was used for the diversity and evenness indices (95% Confidence limit). The non-parametric weighted Spearmans (or Harmonic) rank correlation (ρ_w) was used to test the correlations or measure of strength between the biotic and abiotic similarity matrices determined from the BIO-ENV procedure. In addition, the relationship between biotic and abiotic factors was analysed by a correlation matrix where correlation coefficients for the 16 abundant species (density data) from all three systems were calculated for each environmental variable. The mean monthly values were (n = 38) from all three sites together .

7.3 Results

7.3.1 Composition of the Larval Fish Assemblages

A summary of the abiotic and biotic characteristics of Durban Harbour, Richards Bay Harbour and St Lucia Estuary is given in Table 7.1. The physical and environmental characteristics of each system are very different particularly in terms of overall size, width of entrance channel and the water conditions. The three dominant families in each systems are, interestingly, the same but they differ in their proportions of the total catch and are represented by different dominant species. The proportions of each estuarine-association group also differ with Durban Harbour having the highest density of estuarine-independent taxa, Richards Bay an intermediate and St Lucia the opposite with more estuarine-associated taxa. Since different species dominated in each system, recruitment patterns varied, with the larvae in each estuarine-association group having different proportions. All three environmental variables accounted for some of the variation in larval fish densities in all three systems but to different degrees (Table 7.1).

The mean species diversity index was significantly higher in Durban Harbour (H' = 1.03; F = 8.07, P = 0.001) than at both Richards Bay Harbour (H' = 0.73) and St Lucia Estuary (H' = 0.68) (Figure 7.1). Evenness was significantly greater in Durban Harbour than in St Lucia (J' = 0.65 and J' = 0.47, respectively; F = 3.90, P = 0.03) but not significantly different to Richards Bay Harbour (J' = 0.57).

Figure 7.2 illustrates the patterns of relative species abundances at each site on the basis of species dominance. All three types (A,B,C) show that St Lucia Estuary has a high dominance of a few species i.e. less diverse, with Richards Bay Harbour an intermediate and Durban Harbour being the most diverse. The partial dominance curve (Figure 7.2B) shows that even with the removal of class 1 species the intermediate dominant species are important in structuring the community with St Lucia Estuary still showing the lowest diversity. The cumulative ranked abundance has a smoothing effect on the curves with Figure 7.2C showing most clearly the lower diversity of St Lucia and highest diversity in Durban Harbour, with Richards Bay Harbour being intermediate. The geometric abundance curve further indicates that all the sites have many species with low abundance and a few species with high abundance (Figure 7.3).

Table 7.1. Summary of abiotic and biotic characteristics of Durban Harbour, Richards Bay Harbour and the St Lucia Estuary.

	Durban Harbour	Richards Bay Harbour	St Lucia Estuary
Physical structure			
Position[A]	29°53'S; 31°00'E	28°48'S; 32°05'E	28°23'S; 32°24'E
Size (km^2)	8.9	14.9	±320
Mouth width (m)	230	750	75-150
Mouth depth (m)	12	19	3.6
Water volume ($m^3 \times 10^6$)[B]	13.5	25.0	2.0
Tidal current ($msec^{-1}$)[C]	?	?	0.7
Environmental variables (range)			
Salinity (‰)	33.0-36.0	33.0-36.0	1.0-36.0
Temperature (°C)	19.0-24.5	18.0-25.0	17.5-30.5
Turbidity (NTU)	1.0-28.0	0.4-44.5	10.2-755.0
Dominant families (% of total catch)	Clupeidae (30%) Gobiidae (15%) Engraulidae (2%)	Engraulidae (50%) Gobiidae (37%) Clupeidae (4.2%)	Gobiidae (75%) Clupeidae (19%) Engraulidae (2%)
Dominant species	*H.quadrimaculatus* *S.holodon* Blenniid 1	*S.holodon* Gobiid 12 *T.vitrirostris*	*G.callidus* *G.aestuaria* *C.mossambica*
Estuarine-association (% of total density)			
Estuarine dependent	2.2	20.7	25.2
Partially estuarine dependent	20.5	40.0	74.1
Estuarine independent	77.3	39.3	0.7
Main recruitment period			
Estuarine dependent	winter	summer	autumn
Partially estuarine dependent	spring	winter	late spring, summer
Estuarine independent	late winter; spring	summer	autumn, winter
Developmental stages (% of total density)			
Estuarine dependent			
Young (Pr,Fl)	6.6	12.7	8.9
Old (Po)	2.9	5.2	12.1
Partially estuarine dependent			
Young (Pr,Fl)	6.2	16.4	1.8
Old (Po)	8.5	25.7	76.6
Estuarine independent			
Young (Pr,Fl)	55.1	21.6	0.2
Old (Po)	20.7	18.4	0.5
Significant variables[D] (% contribution to regession model)			
Estuarine dependent	-te, sa (31%)	tu,te (27%)	tu,-sa (45%)
Partially estuarine dependent	none	tu,sa (8%)	tu,te (29%)
Estuarine independent	sa,-tu,-te (22%)	te,tu,sa (27%)	sa,te,cu (8%)

[A] see Fig. 2.1

[B] amount of water entering system over spring flood tide (Forbes *et al.* 1994)

[C] spring flood tide maximum

[D] sa, salinity; te, temperature; tu, turbidity; cu, current

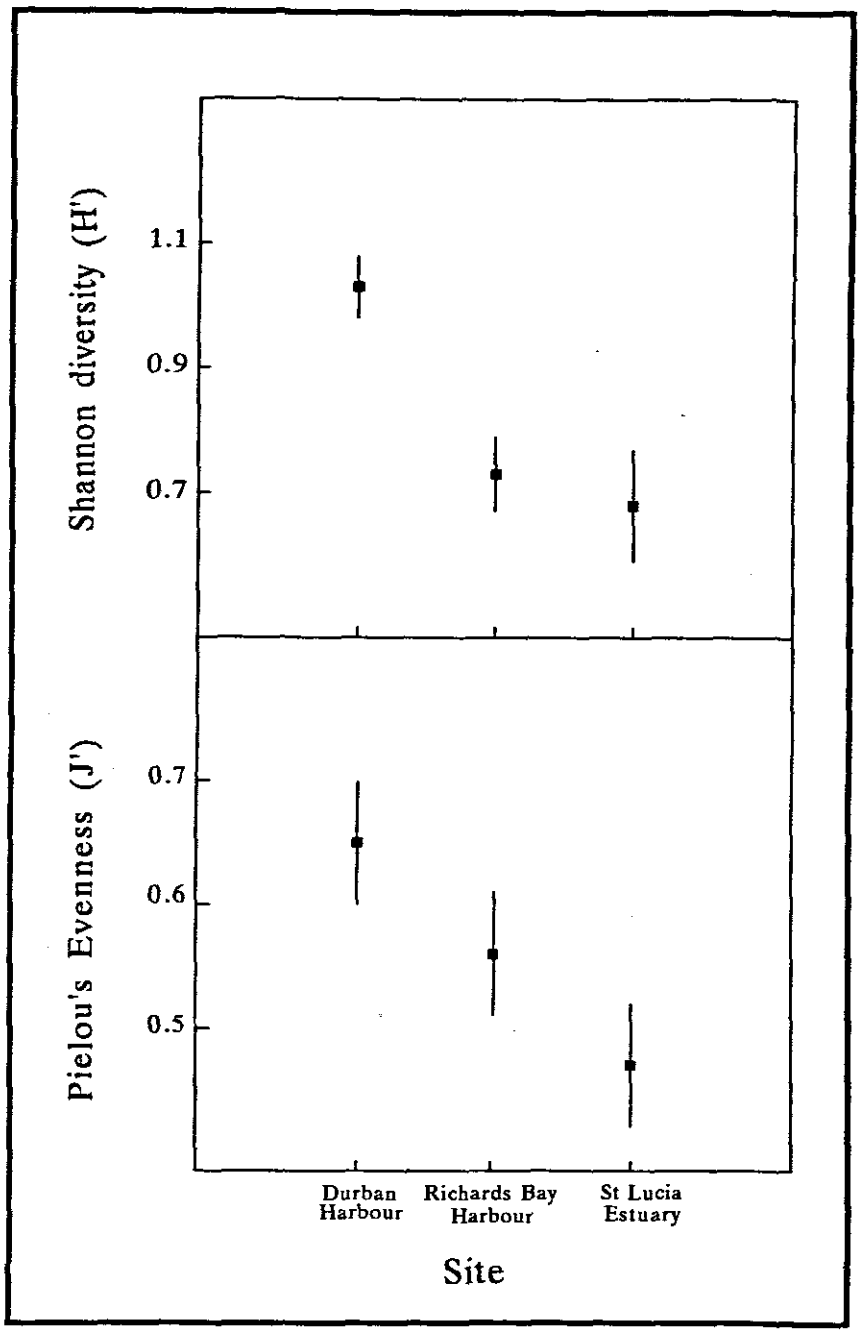


Figure 7.1. Means and 95% confidence intervals for Shannon diversity (H') and Pielou's Evenness (J') at each of the three sites, Durban and Richards Bay Harbours and the St Lucia Estuary shown in Figure 2.1.

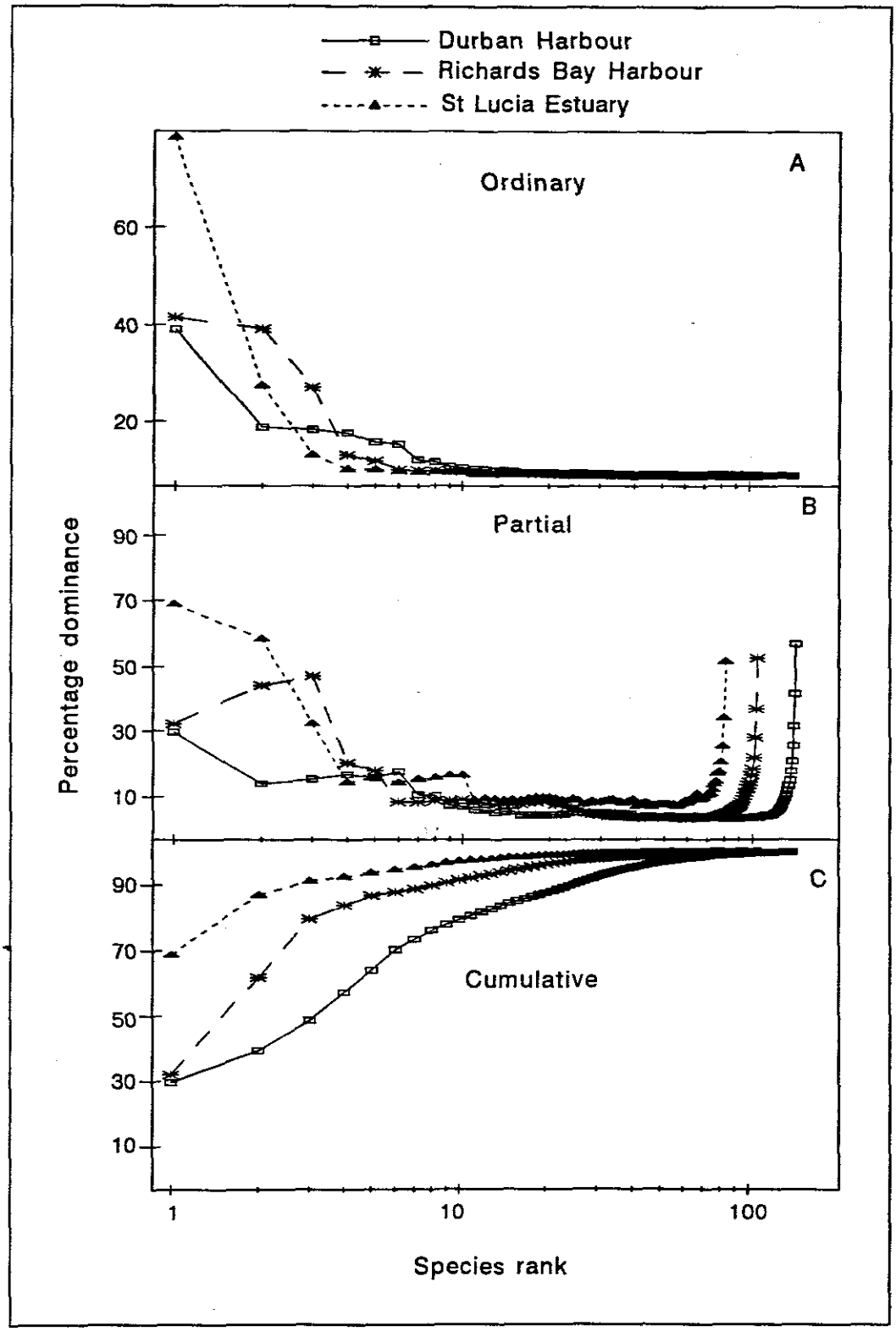


Figure 7.2. Dominance curves (A) ordinary, (B) partial and (C) cumulative for species abundance data from Durban and Richards Bay Harbours and the St Lucia Estuary. Note that the x-axis is on a log scale.

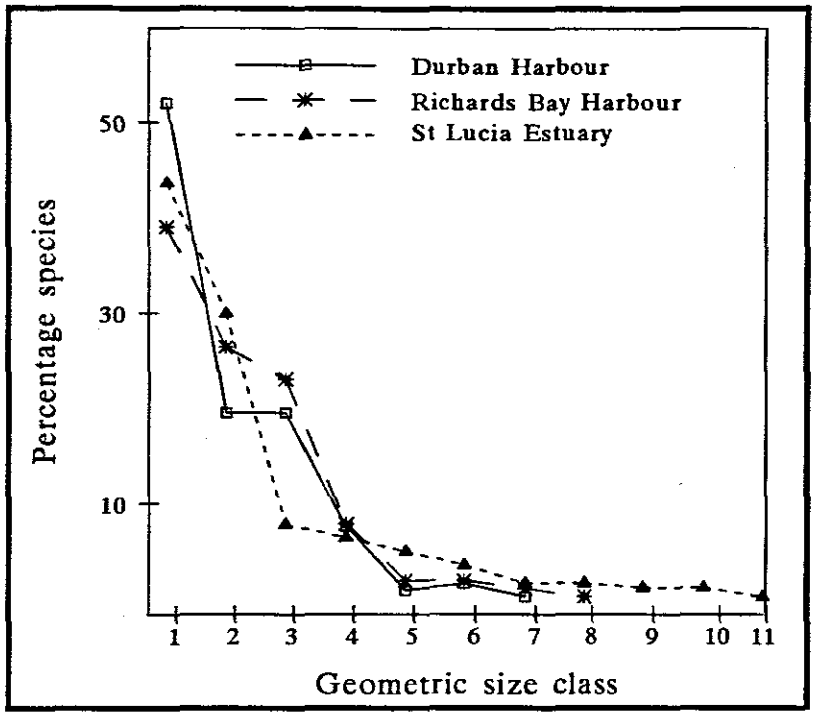


Figure 7.3. Plots of geometric species abundance classes (x 2) for the three sites Durban and Richards Harbours and the St Lucia Estuary.

Classification analysis of larval fish densities at all three sites grouped together into three major clusters which were delineated at the 25-30% similarity level: Group 1 is winter and spring in Richards Bay Harbour; Group 2 is a mixture of Richards Bay and Durban Harbour; Group 3 is all the St Lucia samples together (Figure 7.4A). The split in the Richards Bay samples between two groups suggests distinct assemblages. The results of the MDS using the same similarity matrix in Figure 7.4B gives essentially the same picture with the St Lucia Estuary samples in a separate group and Durban Harbour and Richards Bay Harbour mixed in Group 2 and four Richards Bay Harbour samples in its own group (stress level = 0.14). No clear seasonal trend is evident except for Richards Bay Harbour which separates out into groups representing one or two seasons (Figure 7.4)

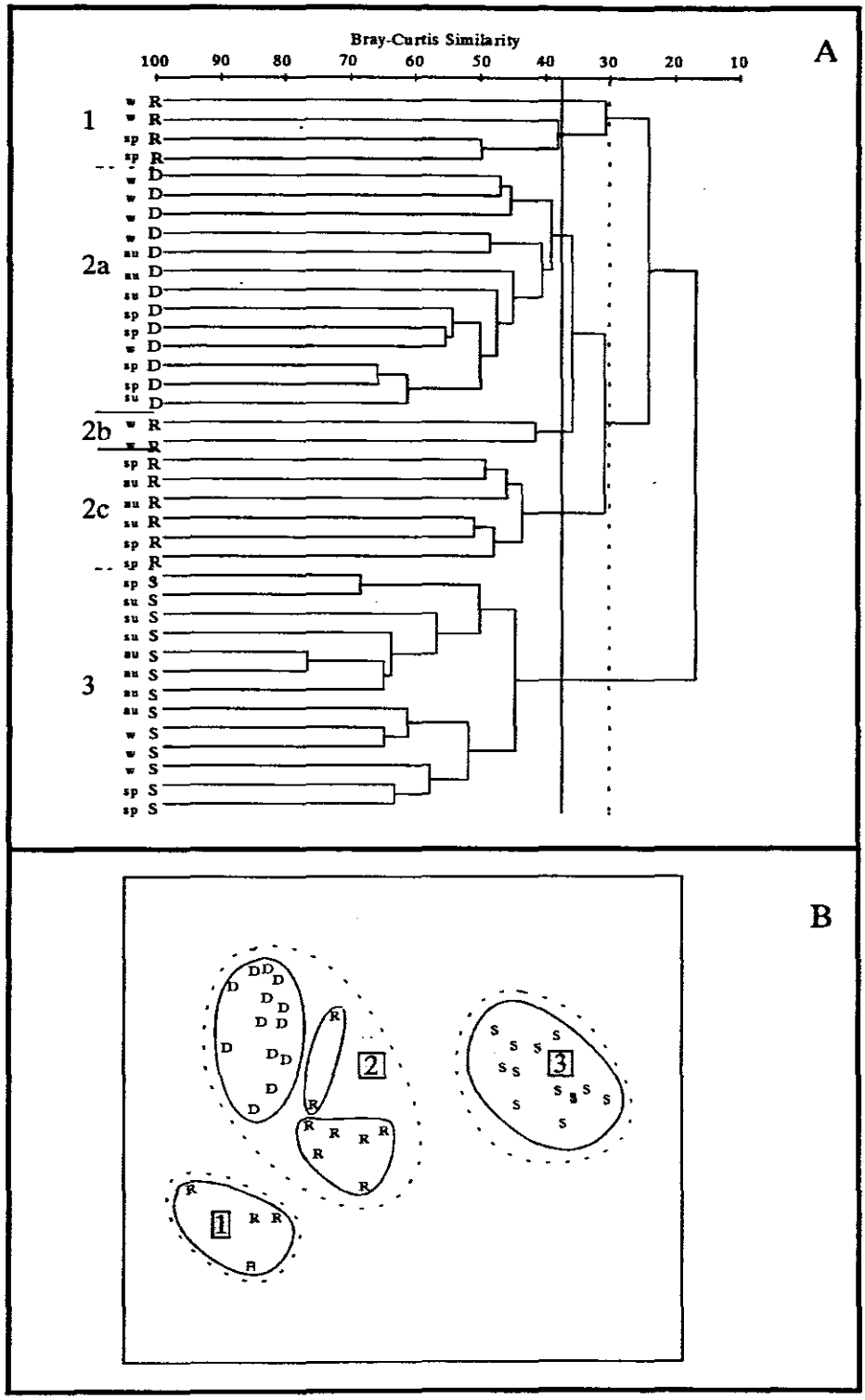


Figure 7.4. Dendrogram (A) showing the clustering of the three sites (D, Durban Harbour; R, Richards Bay Harbour; S, St Lucia Estuary) based on mean monthly abundances, and the ordination in 2-dimensions (B) using MDS on the same similarity matrix. Clusters 1 to 3 and subclusters 2a, 2b and 2c were distinguished from the dendrogram (A) and are indicated by circles in the ordination (B). (w, winter; sp, spring; su, summer; au, autumn).

The species similarity matrix (inverse analysis) clusters into five groups at the 25% similarity level (Figure 7.5A). The species comprising each group, which site each species comes from and the estuarine association category of each species are shown in Table 7.2. The MDS of the same similarity matrix (stress level = 0.18) shows that the groups have separated out according to the degree of estuarine association of a species and hence habitat type (Figure 7.5B): Group 1 is an outlier and is represented by a single unidentified gobiid species from Richards Bay. Group 2 consists of three estuarine associated species present at all three sites; Group 3 species are all estuarine associated, except for *Arothron immaculatus,* and are predominantly from the St Lucia Estuary; Group 4 is a mixture of estuarine-dependent and independent species from all three sites; Group 5 species are all independent of estuaries, except *Pomadasys commersonnii* and *Acanthopagrus berda,* and are mainly from Durban Harbour but also common to Richards Bay Harbour. In summary, most species are strongly related to site groups, although some species are common to two or all three estuarine systems (12 and 3 species, respectively) which results in a gradient of estuarine to marine habitat type i.e. from the St Lucia Estuary to Durban Harbour. The three abundant species common to all three sites were *Croilia mossambica, Solea bleekeri* and *Stolephorus holodon.* The species most responsible for site groupings (SIMPER analysis - see section 7.2) were: *G.callidus, G.aestuaria, S.holodon, C.mossambica* and Gobiid 12 (see Table 7.2).

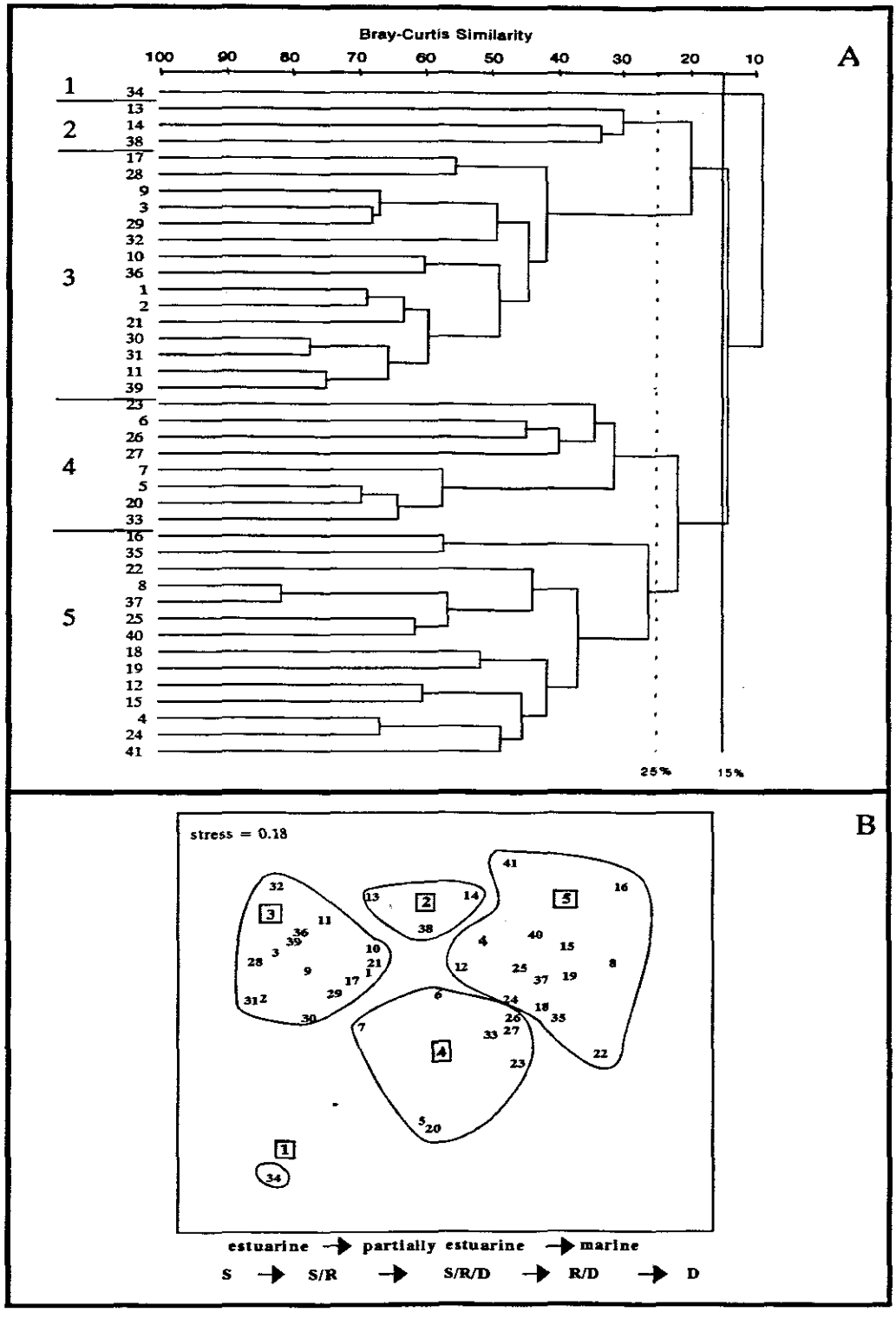


Figure 7.5. Dendrogram (A) showing the inverse analysis clustering based on mean monthly abundances of 41 species occurring in the top 20 ranked species from each site, and the ordination in 2-dimensions (B) using MDS on the same similarity matrix. Clusters 1 to 5 were distinguished from the dendrogram (A) and are encircled in the ordination (B).

Table 7.2. Species groups distinguished by inverse analysis. Species numbers refer to those in both the classification and ordination diagrams (Fig. 7.5) derived from the dominant species matrix (species underlined = species contributing most to similarities in a group)

Group	Species code no.[A]	Species	Est-assoc group[B]	Site[C]
Group 1	34	Gobiid 13	indep	R
Group 2	13	*Rhabdosargus holubi*	est dep	S,R
	14	*Rhabdosargus sarba*	est dep	R,D
	38	*Solea bleekeri*	part est dep	S,R,D
Group 3	17	*Johnius dussumeiri*	part est dep	S,R
	28	*Glossogobius callidus*	part est dep	S
	9	*Hyppichthys heptagonus*	part est dep	S
	3	*Gilchristella aestuaria*	est dep	S
	29	*Redigobius* sp.	est dep	S
	32	Gobiid 4	part est dep	S
	10	*Ambassis* sp.	part est dep	S
	36	Eleotrid 2	est dep	S
	1	*Elops machnata*	est dep	S,R
	2	*Megalops cyprinoides*	est dep	S
	21	*Leiognathus equula*	part est dep	S
	30	*Taenioides esquivel*	part est dep	S,R
	31	*Taenioides jacksoni*	est dep	S
	11	*Terapon jarbua*	est dep	S
	39	*Arothron immaculatus*	indep	S,D
Group 4	23	*Omobranchus* sp.	indep	R
	6	*Stolephorus holodon*	part est dep	S,R,D
	26	*Draculo celatus*	indep	R,D
	27	*Croilia mossambica*	part est dep	S,R,D
	7	*Thryssa vitrirostris*	est dep	S,R
	5	*Pellona ditchella*	indep	R
	20	Sciaenid 2	indep	R
	33	Gobiid 12	indep	R,D
Group 5	16	*Nemipterus* sp.	indep	D
	35	Gobiid 27	indep	R,D
	22	*Secutor insidiator*	indep	D
	8	*Cyclothone pseudopallida*	indep	D
	37	*Cynnoglossus* sp.1	indep	D
	25	Tripterygiid 1	indep	D
	40	*Lampanyctus alatatus*	indep	D
	18	*Argyrosomus* sp.	IIb?	D
	19	*Umbrina ronchus*	indep	D
	12	*Pommadasys commersonnii*	est dep	R,D
	15	*Acanthopagrus berda*	est dep	R
	4	*Hercklotsichthys quadrimaculatus*	indep	R,D
	24	Blenniid 1	indep	R,D
	41	*Scopelosis multipunctatus*	indep	D

[A]species code numbers derived from classification and ordination (Fig. 7.5)

[B]est-dep, estuarine-dependent; part est-dep, partially estuarine-dependent; indep, estuarine-independent

[C]present in Durban Harbour (D), Richards Bay Harbour (R) and the St Lucia Estuary(S), for the dominant species matrix only.

7.3.2 Relationship of Site Groups to Environmental Variables

Figure 7.6. is an ordination representing the same site groups from Figure 7.4B with the environmental variables, salinity, temperature and turbidity, superimposed on the sites. It shows clearly that each site is characterised by particular water conditions: the St Lucia Estuary has a greater range of salinities and temperatures with considerably higher turbidities than Durban and Richards Bay i.e. a 'typical' estuarine physical environment. Durban and Richards Bay Harbours have very similar environmental conditions with essentially marine salinities and low turbidities, but with turbidities being higher in some months in Richards Bay Harbour (Figure 7.6).

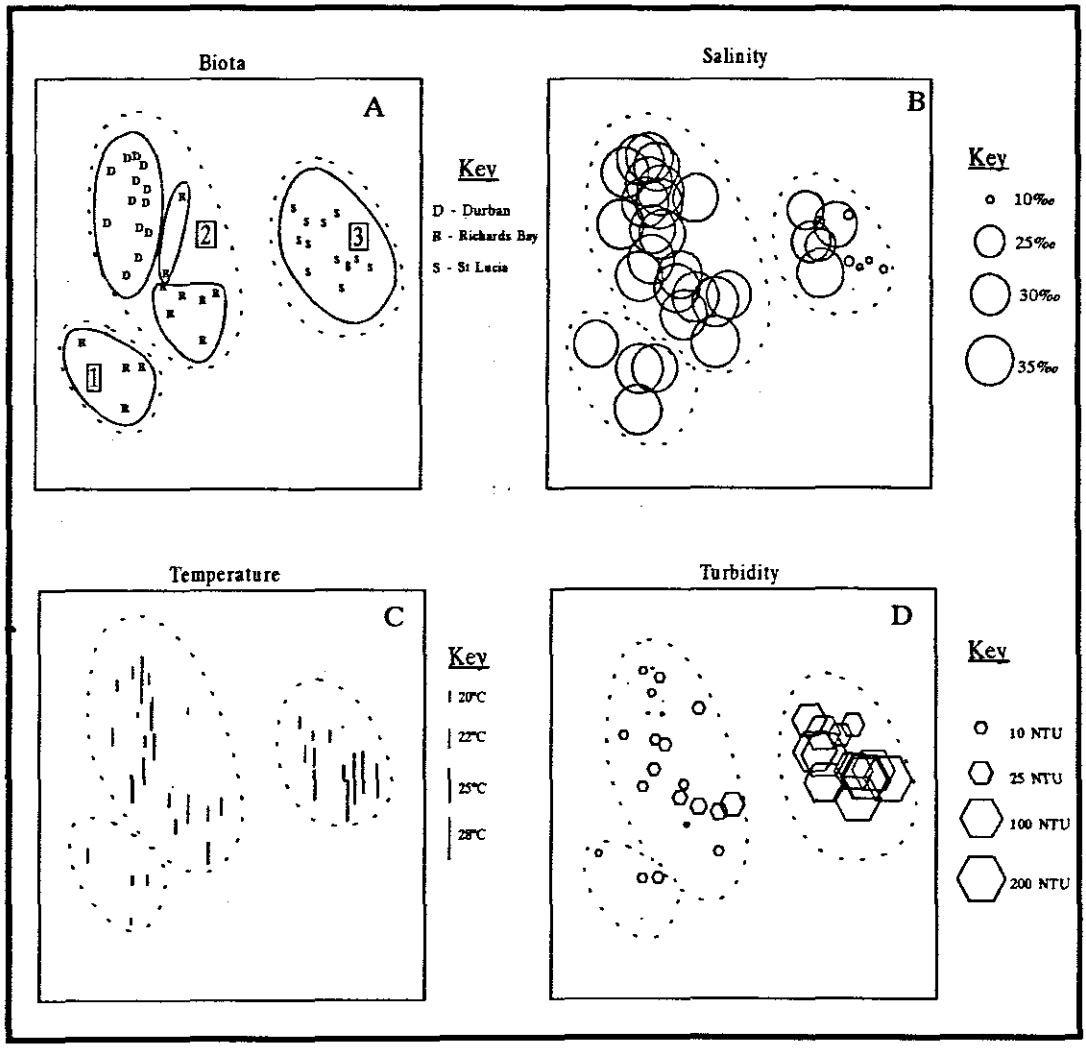


Figure 7.6. MDS of species abundances at the three sites (A) (D, Durban Harbour; R, Richards Bay Harbour; S, St Lucia Estuary). (B) - (D) are the same MDS but with superimposed symbols representing salinity, temperature and turbidity mean monthly values at each site.

The ordinations in Figure 7.6 suggested that some intercorrelation exists between the environmental variables since the gradients (either positive or negative) of each variable are similar i.e. a high to low salinity gradient in relation to a low to high turbidity gradient. The "best fitting" environmental variables which explains the community pattern was turbidity on its own (weighted Spearman's rank correlation, $\rho_w = 0.55$) followed by the combinations of salinity + turbidity ($\rho_w = 0.48$), temperature + turbidity ($\rho_w = 0.42$), salinity + temperature + turbidity ($\rho_w = 0.41$), and salinity + temperature($\rho_w = 0.25$) (Figure 7.7B - F).

The relationship of larval densities to environmental conditions was shown to be species-specific. Densities of the 16 most abundant species from all three sites were correlated to the abiotic factors in varying degrees (Table 7.4).

Table 7.3. Correlation coefficients (R) between 16 abundant species and the environmental variables. (95% confidence limits).

Species abbreviation[A]	Species	Salinity (‰)	Temperature (°C)	Turbidity (NTU)
G.a	*Gilchristella aestuaria*	-0.86***	0.62***	0.84***
T.j	*Taenioides jacksoni*	-0.56	0.64***	0.47***
G.c	*Glossogobius callidus*	-0.90***	0.68***	0.88***
T.e	*Taenioides esquivel*	-0.36*	0.53**	0.38*
Am	*Ambassis* sp.	-0.60	0.57***	0.70***
E.m	*Elops machnata*	-0.65***	0.50*	0.71***
T.v	*Thryssa vitrirostris*	-0.21	0.52**	0.38*
S.b	*Solea bleekeri*	-0.14	-0.26	0.13
P.c	*Pomadasys commersonnii*	0.18	-0.08	-0.09
S.h	*Stolephorus holodon*	0.25	0.02	-0.08
G27	Gobiid 27	0.28	0.15	-0.34*
H.q	*Herklotsichthys quadrimaculatus*	0.34*	-0.11	-0.46**
G12	Gobiid 12	0.45**	-0.06	-0.47**
C.m	*Croilia mossambica*	0.46**	-0.01	-0.46**
T1	Tripterygiid 1	0.30	-0.14	-0.47**
B1	Blenniid 1	0.39*	-0.19	-0.58***

[A]Species abbreviations as shown in Figure 7.8
*P<0.05;**P<0.01; ***P<0.001

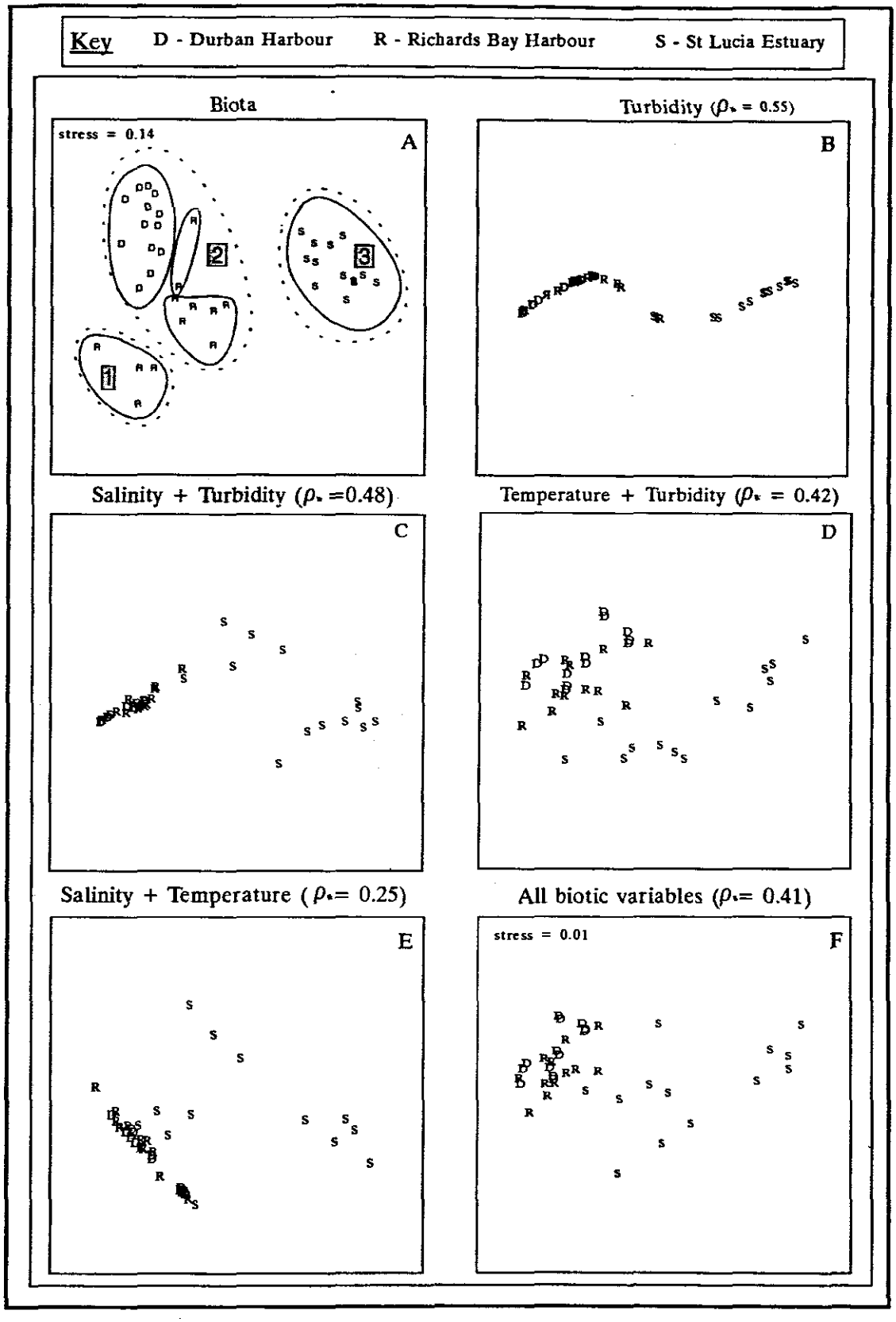


Figure 7.7. MDS ordinations of the three sites (D, Durban Harbour; R, Richards Bay Harbour; S, St Lucia Estuary) on (A) species abundances, (B) turbidity, (C) salinity + turbidity, (D) temperature + turbidity, (D) salinity + temperature, (E) all abiotic variables.

The correlation coefficients between the species and environmental variables are plotted on a correlation matrix (Figure 7.8). This shows, firstly, that the response of biotic on abiotic factors is species-specific and, secondly, estuarine associated species group together on the correlation matrix as do the marine species. Estuarine species (e.g. *Glossogobius callidus, Gilchristella aestuaria* and *Taenioides jacksoni*) plotted in the 1st quadrant (estuarine) have strong positive correlations with temperature and turbidity but negative correlations with salinity (Figure 7.8). Marine species (e.g. *Herklotsichthys quadrimaculatus*, Blenniid 1 and Tripterygiid 1), on the other hand, are plotted in the 4th quadrant (marine) which has negative correlations with temperature and turbidity and positive correlations with salinity. This illustrates clearly that the abundance of fish larvae of different species is influenced to some degree by changes in environmental water conditions.

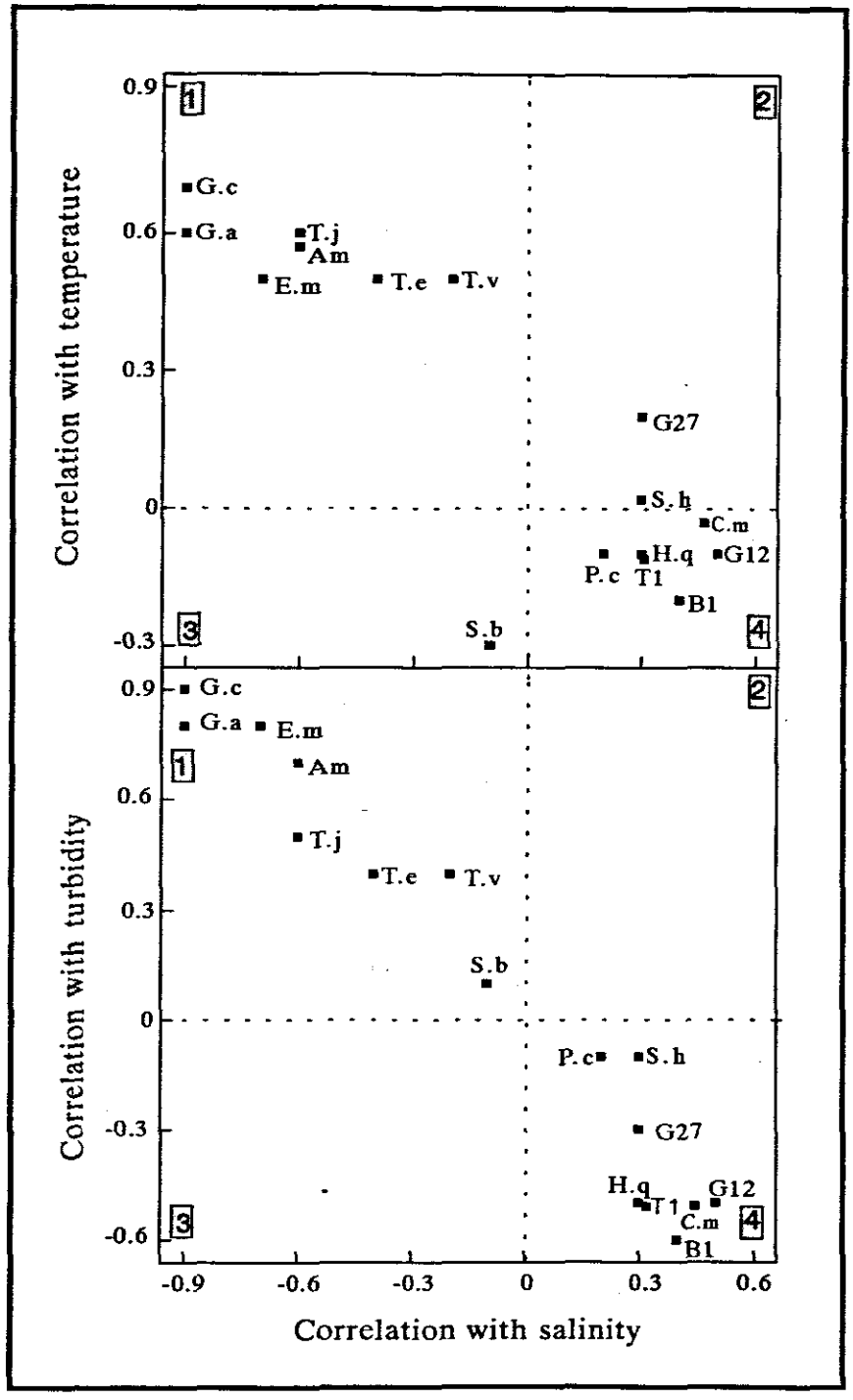


Figure 7.8. Correlation coefficients (R) plotted against salinity (x-axis), temperature and turbidity (y-axis). Dotted lines indicate 4 quadrants which correspond to habitat type: 1 - estuarine; 2 - semi-estuarine; 3 - semi-marine; 4 - marine.

7.4 Discussion

7.4.1 Structure and Composition of the Larval Fish Assemblages

Increasing levels of environmental stress (disturbance) have generally been considered to decrease diversity and evenness but increase abundance (Clarke and Warwick 1994). The diversity and evenness indices, in addition to the dominance curves determined for the larval fish assemblages in the present study, indicated that the community in the St Lucia Estuary is characterised by a high dominance of a few species, in comparison with the two harbour systems. This implies that St Lucia Estuary is a more perturbed and stressed habitat, however, the reason for the lower diversity is more likely a consequence of the non-penetration of marine species into St Lucia. Anthropomorphic disturbances would probably exacerbate the instability of St Lucia . The system has changed drastically over the last 50 years due to human interference (Wright and Mason 1993) such as poor farming techniques in the Umfolozi River catchment and channelizing of the Umfolozi River flood plain resulting in high sedimentation rates and closure of the estuary mouth from April 1951 to April 1956.

A decrease in species diversity is also associated with increased harshness or unpredictability of abiotic conditions (Sanders 1968). Southern African estuaries are characterised by being ephemeral, unpredictable habitats in which the species composition of fish communities is of a low diversity with a high abundance of only a few taxa (Whitfield 1994b). Despite this physical instability, the species composition of juvenile and adult fish within these systems is relatively stable with the fish having more or less predictable patterns of abundance and distribution (Day *et al.* 1981). Studies on the juvenile and adult fish assemblages in Durban and Richards Bay Harbours showed that the fish species diversity was unexpectedly high, particularly Durban Harbour, (Hay *et al.* 1995). They concluded that despite the semi-natural estuarine environment of these Harbours both systems are in a relatively good ecological condition and fairly stable. In the present study, the partial dominance curves show that it is a "suite" of

species responsible for structuring the assemblage i.e. even with the removal the few particularly abundant species the patterns of dominance are still apparent. Morais and Morais (1994) found that the larval and juvenile fish assemblage in the tropical Cayenne River Estuary (French Guiana, South America) was apparently stable, with a moderate species diversity of H' = 1.68 at the site near the mouth of the estuary. The authors cautioned that this may be an overestimate since the Shannon-Wiener index is sensitive to the presence of rare species i.e. many taxa represented by only a few individuals. Other workers have recorded high ichthyoplankton diversity near the mouth of estuaries (Pearcy and Myers 1974; Miskiewicz 1987; Neira *et al.* 1992; Tzeng and Wang 1992).

Wootton (1990) describes a fish assemblage as being essentially unpredictable and not attaining equilibrium state which results in a stochastic community. A larval fish assemblage would be particularly stochastic since it comprises the pelagic stage of fishes and movement in the water column and so currents play an important role. The larval assemblages in the present study are distinct in each system but must change in composition and abundance on a seasonal basis. Coastal larval fish assemblages are also identifiable but are dynamic with both their boundaries and composition changing over time (Cowen *et al.* 1993). The latter authors found that the maintenance of the assemblage boundaries is due to a combination of the physical features of the environment and ontogenetic behavioural patterns. Biological interactions such as food availability, predation and competition must also play a part in structuring these communities.

The main forces structuring the assemblages in Durban, Richards Bay harbours and St Lucia Estuary are the interactive effects of the physical environment and differing responses of the different species to environmental conditions. Habitat type and topography are important factors determining ichthyofaunal assemblage structure (Leis 1993; Blaber *et al.* 1995). The classification and ordination showed clearly that the larval assemblage in each of the three systems is structured differently with a gradient existing from low diverse/high abundance → more diverse/lower abundance i.e.

estuarine → semi-estuarine → marine (Figure 7.5). This difference is, in part, due to the different physical structures of each system (Table 7.1). The two harbours have similar salinity and temperature ranges but Richards Bay has a relatively wider turbidity range. Although the entrance of Richards Bay Harbour is substantially wider with a greater tidal exchange than that of Durban Harbour, the larval fish assemblage is semi-estuarine. This may be due to the fact that Richards Bay Harbour is a more recent harbour - the development of Durban Harbour began in 1850s whilst Richards Bay was only established as a harbour in 1970. Classification of the ichthyofauna of southern African estuaries showed that Richards Bay was an outlier distinct from that of the warm- and cold-temperate estuaries (Whitfield *et al.* 1989).

The separation of the different species into certain groups related to site differences is indirectly related to the degree of estuarine-association of a species (Felley 1987). Detrended correspondence analysis differentiated between freshwater and estuarine assemblages found in different regions of the system. The inverse analysis of the present study, demonstrates that species groups occur along a gradient from typically estuarine (estuarine spawners) → partially estuarine (estuarine and marine spawners) → marine (marine spawners). However, certain species are common to all three or just two of the systems. Felley (1987) also found that the freshwater and estuarine assemblages had some species in common.

Part of the process of discriminating sites in multivariate studies is the ability to identify the species most responsible for the observed pattern (Clarke and Warwick 1994). Five main species were responsible for the observed grouping patterns in the present study: *G.callidus*, *G.aestuaria*, *S.holodon*, *C.mossambica* and Gobiid 12 (Table 7.2). It is the differences in each of these species habitat preferences that have separated them out into certain groups. For instance, *G.callidus* and *G.aestuaria* are species strongly associated with estuaries, *S.holodon* and *C.mossambica* with both estuaries and the marine environment, and Gobiid 12 was most abundant at sea. Field *et al.* (1982) found that for estuarine benthic communities the species were confined to their

respective station groups because of certain biochemical, physiological, morphological or behavioural adaptations. This certainly applies to the present study, since, larvae of the river goby (*G.callidus)* and the estuarine round-herring (*G.aestuaria*) were confined to low salinity, and high temperature and turbidity conditions (Figure 7.8). Tzeng and Wang (1992) similarly found that larvae of certain species (e.g. *Thryssa kammalen, Ambassis gymnocephalus, Elops hawaiensis*) were more associated with the freshwater conditions (low salinity and high temperature) at the head of the Tanshiu River Estuary.

7.4.2 Environmental Factors Structuring the Larval Fish Assemblages

The nature and density of the fish fauna in southern African estuaries varies from one system to another because of the environmental differences between the estuaries (Day *et al.* 1981). A number of factors must play a role in determining the structure and composition of a larval fish community occurring within southern African estuaries, for example:

- zoogeography determines which species are available for recruitment and is related to location of spawning sites
- condition of estuary mouth which is related to the amount of tidal exchange.
- variations in environmental conditions.

Results from the present study indicated that variations in environmental conditions plays a major role in structuring the larval fish assemblages in estuarine environments. South African estuaries are unpredictable habitats where conditions such as salinity, temperature, turbidity, currents and dissolved oxygen can fluctuate rapidly (Whitfield 1990). The larval stages of fishes have greater sensitivity to changes in environmental conditions compared with later stages (McKim 1984). In addition, the dynamics of a larval fish community in response to environmental change depend upon the responses

of the individual species that make up the community. In the tropical Tanshui River Estuary the abundance of fish larvae and early juveniles was greatly influenced by the changes in salinity and temperature and was species-specific (Tzeng and Wang 1992). The present study clearly indicated similar responses of the fish larvae to changing environmental conditions.

The importance of environmental variables in influencing larval abundance patterns is now established, but which variable is most important ? By superimposing the environmental variables on the site samples it was shown that, of the three variables measured in the present study, turbidity was the most important variable responsible for grouping the site samples. However, single variables alone cannot account for the observed patterns in larval fish abundance and it is the intercorrelation between a number of environmental factors determining these patterns. This was evident from both the stepwise regression analysis from Chapters 4,5 and 6 and the multivariate analyses in the present Chapter. Other factors which may play an important role are current velocities and certain water quality parameters such as pH and dissolved oxygen (DO). The latter variables have been shown to influence fish larvae and juvenile abundances in estuaries (Tzeng and Wang 1992; Blaber *et al.* 1995).

In summary, a combination of controlling factors play a part in structuring the larval fish assemblages in all three estuarine systems. Figure 7.9 gives a schematic representation of the three types of larval fish assemblages which have been identified in the present study. The St Lucia Estuary represents a more typical estuarine habitat than the two harbours with fluctuating water conditions exacerbated by bad catchment management and recreational activities. The larval fish assemblage is, therefore, characterised by the dominance of a few very abundant species. Richards Bay Harbour is an intermediate system where water conditions are less harsh and semi-estuarine but it is still a relatively recent harbour where some typical estuarine condition still prevail. Durban Harbour has increased stability since harbour development has resulted in a poermanently open entrance channel and, therefore, has essentially marine conditions.

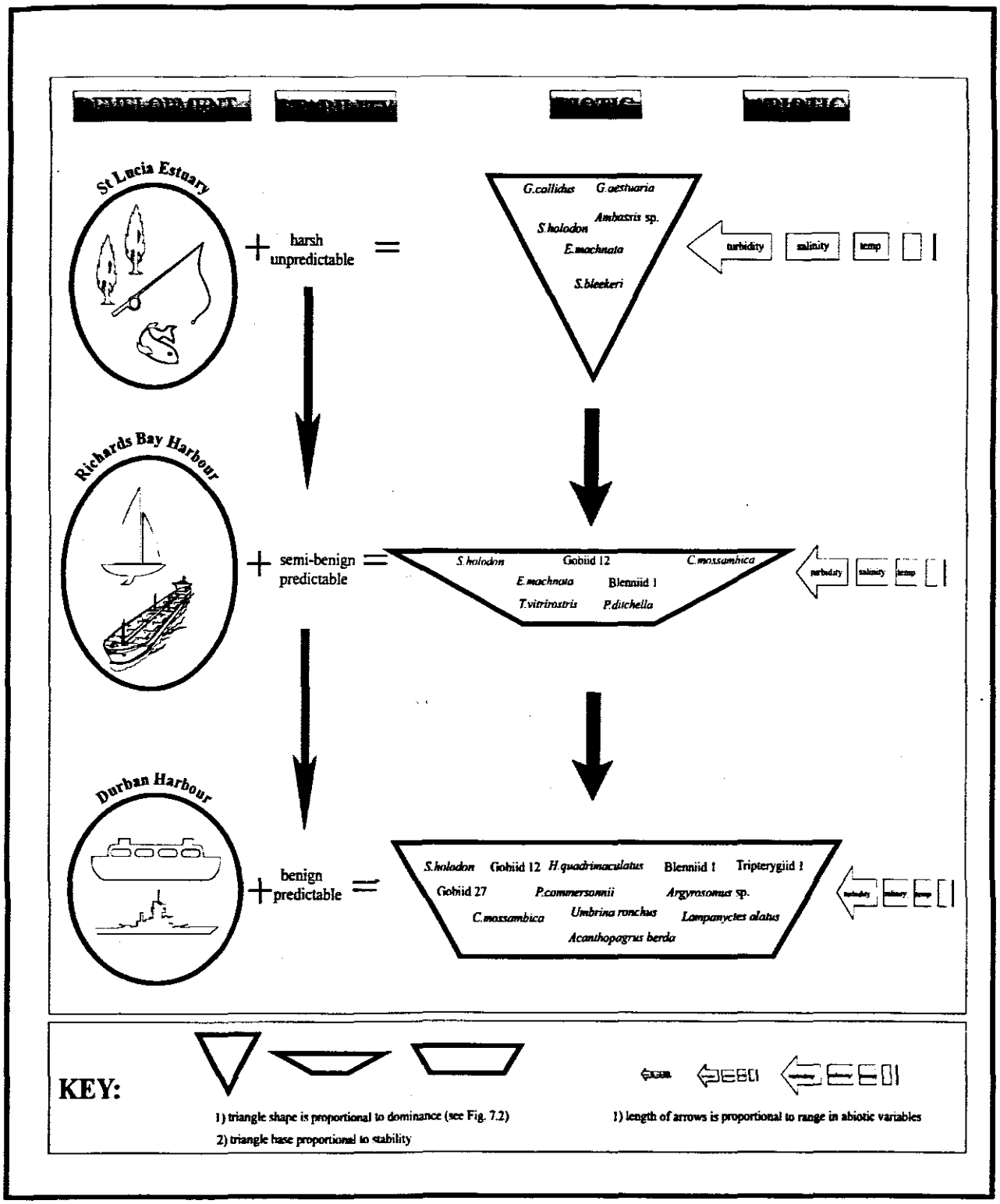
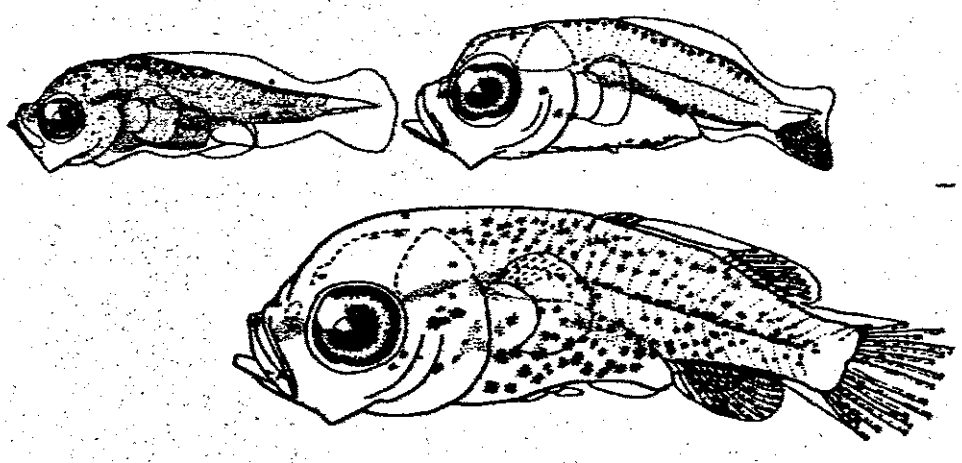


Figure 7.9. Schematic representation of the three types of larval fish assemblages identified in the present study.

CHAPTER 8

Larval and Juvenile Fishes in the Surf Zone Adjacent to th St Lucia Estuary Mouth



8. LARVAL AND JUVENILE FISHES IN THE SURF ZONE ADJACENT TO THE ST LUCIA ESTUARY MOUTH

8.2. Introduction

It is well established that many coastal marine fish species utilize specific nursery areas during the juvenile stage of their life-cycles. In southern Africa, estuaries (Wallace and van der Elst 1975; Day *et al.* 1981; Beckley 1984; Blaber 1985; Whitfield and Kok 1992), surf zones (Lasiak 1981; Bennett 1989b; Clark *et al.* 1994), nearshore reefs (van der Elst 1981) and tide pools (Beckley 1985, Bennett 1987; Beckley 1994) have been identified as nursery areas for several coastal fish species. In comparison with south-western Australia, southern Africa has relatively few inshore areas which can function as nursery areas and so estuarine systems are vital in the recruitment of many fish species (Potter *et al.* 1990). Surf zones adjacent to sandy beaches are also important as nursery habitats for certain marine fish in south-western Australia (Lenanton 1982; Ayvazian and Hyndes 1995) and the northern Gulf of Mexico (Modde 1980; Modde and Ross 1981).

Studies by Lasiak (1981, 1984a,b, 1986), on the surf zone fish assemblage at King's Beach in the Eastern Cape, indicated early recruitment of the majority of species since many small juveniles were caught. Subsequent studies from the same region have shown that larval stages (mainly postflexion) of estuarine-associated marine species were abundant in the surf zone (Whitfield 1989c). Other studies on ichthyoplankton in surf zones have been undertaken in the northern Gulf of Mexico (Ruple 1984) and Japan (Senta and Kinoshita 1985; Kinoshita 1986; Kinoshita and Fujita 1988; Morioka *et al.*1993). The difficulty in sampling ichthyoplankton in a surf zone, particularly on high energy coastlines, is self-evident and sampling methods have generally involved the use of a handheld "push net" (Ruple 1984; Whitfield 1989; Morioka *et al.* 1993) or a some type of fine-meshed seine net (Senta and Kinoshita 1985; Kinoshita 1986; Kinoshita and Fujita 1988).

The first phase of movement necessary for recruitment to estuaries by fish species spawned offshore is the accumulation of larvae in the nearshore coastal zone (Boehlert and Mundy 1988). These larval and juvenile stages tend to accumulate in the vicinity of estuary mouths (Whitfield 1989b; Potter *et al.* 1990) although Clark *et al.*(1994) found

that there was no relationship between juvenile fish density and distance from river mouths. In studies of fish recruitment to estuaries, researchers often attempt to correlate spatial and temporal patterns of distribution with physical variables to infer the behavioural response by the immigrating fish (Boehlert and Mundy 1988).

The aim of the present study was to determine the role of the surf zone, adjacent to the St Lucia Estuary mouth, in the early life history stages of estuarine-associated fish species. Species composition, seasonality and diel changes in abundance were investigated and developmental stages noted to determine size at entry into the surf zone. The estuarine-association categories (Whitfield 1994a) for all taxa were also noted to assess the importance of the surf zone habitat as a nursery area. The estuary mouth was closed for the last three months of the study and so an additional 24-h study was undertaken in the surf zone opposite the sand bar blocking the estuary mouth i.e. to ascertain any diel patterns in abundance and presence of estuarine-associated species. Relationships between environmental variables and fish densities were also examined.

8.2. Results

8.2.1 Environmental Variables

During the 12-month surf zone study, adjacent to the St Lucia Estuary mouth (Figures 2.4 and 2.6, Chapter 2), mean monthly salinities of the water varied from 34.0‰ in June to 36.0‰ in February and March (Figure 8.1). Mean temperatures varied seasonally with a minimum of 20.2°C in winter (August) and a maximum of 27.0°C in summer (February). No significant differences in temperature or salinity were found between day and night measurements, however, significant differences between sampling dates were recorded (both $P < 0.05$, $F = 133.16$ and $F = 100.53$, respectively). Mean monthly turbidity was low in winter (3.7 NTU) with higher values being recorded in spring (16.4 NTU), summer (11.3 NTU) and autumn (13.3 NTU) (Figure 8.1). Turbidity values were significantly higher in day samples ($P = 0.023$, $F = 5.48$).

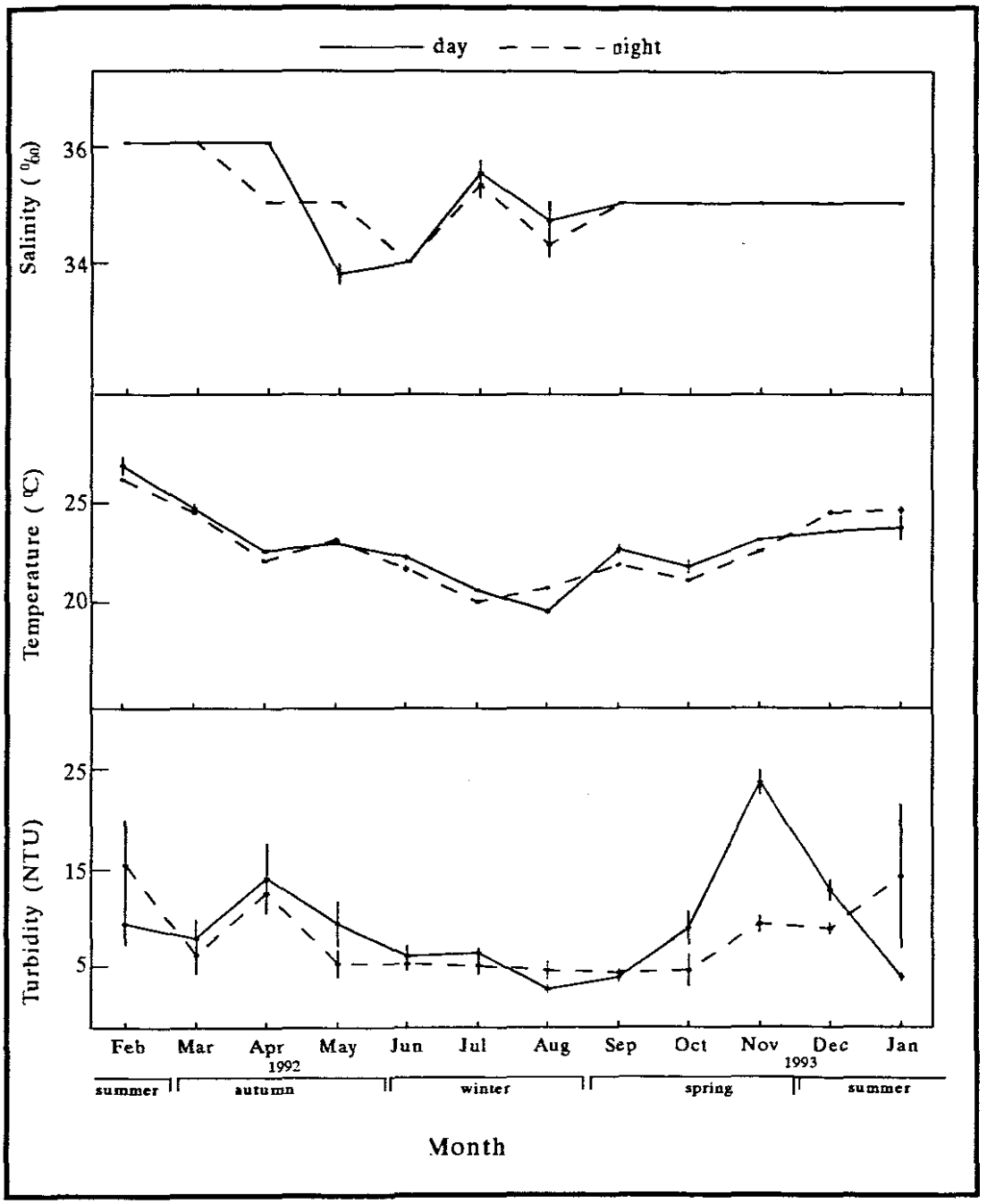


Figure 8.1. Mean monthly variations (± 1SE) of the environmental variables (salinity, temperature and turbidity) for top, mid and bottom samples in the surf zone adjacent to the St Lucia Estuary mouth, from February 1992 to January 1993.

8.2.2. Assemblage Composition and Relationships to Environmental Variables

A total of 2 931 larvae and juveniles, representing 88 taxa and 47 families, was collected from February 1992 to January 1993 (Table 8.1). The most abundant larvae belonged to the families Sparidae, Haemulidae, Ambassidae, Tripterygiidae and Chanidae together contributing 64.2% of the total catch (Figure 8.2). Other families contributing between 2 and 6% of the total catch were the Elopidae, Notocheiridae, Mugilidae, Teraponidae and Scombridae. The most abundant species were the grunter *Pomadasys olivaceum*, the glassy *Ambassis* sp. and the seabream *R.holubi*. Other abundant species (contributing between 3 to 10% of the total catch) were Tripterygiid 1, *C.chanos*, *Diplodus sargus capensis*, *E.machnata*, *A.berda* and *Iso natalensis* (Table 8.1).

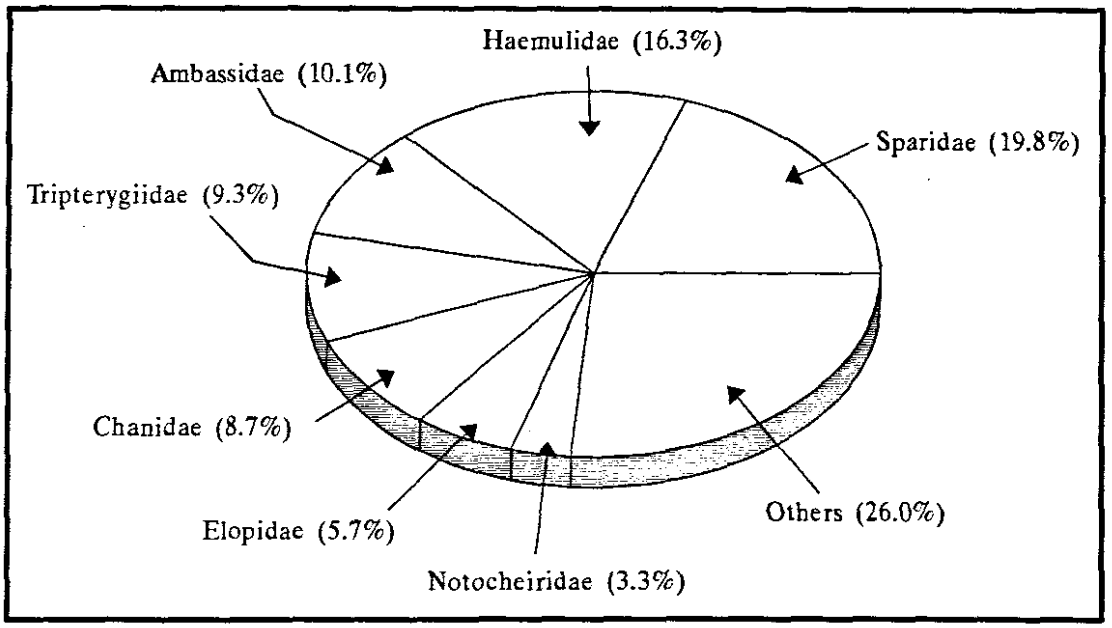


Figure 8.2. Percentage contribution of dominant families for all taxa collected in the 12-month surf zone study.

Table 8.1. Total catch, body length and developmental stage for all larval and juvenile fish taxa collected he 12-month study in the surf zone (adjacent to the St Lucia Estuary mouth. Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile; D, day; N, night - *abundant, **very abundant)

Family	Species	Rank overall	Total catch no	Total catch mean no.100m^{-3}	Total catch %	Body length (mm) mean	Body length (mm) range	Developmental stage	Presence	Ju & Ad present [A]
ESTUARINE-DEPENDENT										
Estuarine residents										
Clupeidae	*Gilchristella aestuaria*		1	0.01	<0.1	22.0		Po	N	+
Gobiidae	*Taenioides jacksoni*		1	0.01	<0.1	10.5		Po	N	
Eleotridae	Eleotrid 2	13	48	0.62	1.8	15.0	13.0-17.0	Po	D*,N*	
Marine spawners dependent on estuaries										
Elopidae	*Elops machnata*	7	164	2.03	5.7	31.2	25.0-34.5	Le	D*,N**	+
Engaulidae	*Thryssa vitrirostris*		4	0.05	0.2	17.7	17.0-18.0	Po	D,N	+
Teraponidae	*Terapon jarbua*	11	60	1.03	2.9	10.8	5.5-13.0	Po	D,N*	
Sparidae	*Acanthopagrus berda*	8	104	1.26	3.6	10.1	8.0-12.2	Po	D,N*	+
	Rhabdosargus holubi	3	290	3.54	10.0	10.8	9.0-12.5	Po	D,N**	+
	Rhabdosargus sarba		8	0.11	0.3	8.4	3.5-11.5	Pr,Po	D,N	+
Monodactylidae	*Monodactylus argenteus*	20	19	0.22	0.6	5.7	5.0-7.0	Po	D,N	+
PARTIALLY ESTUARINE-DEPENDENT										
Catadromous										
Megalopidae	*Megalops cyprinoides*		18	0.19	0.5	25.7	24.0-28.5	Le	D,N*	+
Estuarine and marine spawners										
Synganthidae	*Syngnathus* sp.		5	0.06	0.2	25.4	9.0-54.0	Po,Ju	D,N	+
Ambassidae	*Ambassis* sp.	2	332	3.56	10.1	6.6	4.0-23.0	Po,Ju	D**,N**	+
Gobiidae	*Croilia mossambica*	14	41	0.56	1.6	10.9	5.5-12.0	Po	D,N*	
	Trypauchen microcephalus		1	0.01	<0.1	10.5		Po	N	+
	Gobiid 1	17	32	0.40	1.1	6.4	4.0-10.5	Pr,Po	D,N*	
Marine spawners with juveniles abundant in estuaries										
Mugilidae	Mugilid spp	10	77	1.03	2.9	11.5	6.0-24.0	Po,Ju	D,N*	+
Soleidae	*Solea bleekeri*	18	21	0.27	0.8	4.5	4.0-5.2	Po	N	+
Marine spawners with juveniles at sea and in estuaries										
Engraulidae	*Stolephorus holodon*	15	44	0.55	1.6	15.7	7.2-27.0	Pr,Fl,Po,Ju	D,N	+
Chanidae	*Chanos chanos*	5	385	3.08	8.7	12.2	10.0-17.2	Po	D*,N**	+
Platycephalidae	*Platycephalus indicus*		2	0.02	0.1	10.3	9.5-11.0	Po	D	+
Sparidae	*Diplodus sargus capensis*	6	162	2.09	5.9	11.8	9.0-21.0	Po,Ju	D,N**	+
Gerreidae	*Gerres* sp.1	19	10	0.23	0.7	9.3	8.0-9.8	Po	N	+

cont.

Table 8.1 cont.

Sillaginidae	*Sillago sihama*		13	0.22	0.6	11.0	5.5-14.0	Po	D,N	+
Sciaenidae	*Johnius dussumieri*		12	0.14	0.4	8.6	6.8-11.0	Po	D,N	+
Leiognathidae	*Leiognathus equula*		4	0.05	0.1	12.5	11.0-14.0	Po	N	+
Sphyraenidae	*Sphyraena jello*		1	0.01	<0.1	20.0		Po	N	+
ESTUARINE-INDEPENDENT[B]										
Reef and shore taxa										
Clupeidae	*Herklotsichthys quadrimaculatus*	16	43	0.49	1.4	18.5	12.0-25.0	Fl,Po	D,N*	
Engraulidae	*Thryssa setirostris*		3	0.06	0.2	29.5	24.0-55.0	Po,Ju	N	+
Gobiesocidae	*Lepadichthys* sp.2		5	0.06	0.2	6.3	5.0-8.0	Po	N	
Notocheiridae	*Iso natalensis*	9	93	1.16	3.3	13.9	5.0-35.5	Pr,Fl,Po,Ju	D,N*	
Syngnathidae	*Hyporhamphus improvisus*		5	0.08	0.2	7.4	6.0-9.0	Po	D	+
Haemulidae	*Pomadasys olivaceum*	1	407	5.74	16.3	12.9	7.5-36.0	Po,Ju	D*,N**	
Scorpididae	*Neoscorpis lithophilus*		18	0.22	0.6	13.9	11.0-15.5	Po	D,N	
Leiognathidae	*Secutor insidiator*		5	0.12	0.3	25.6	22.0-28.0	Po,Ju	N	+
Blenniidae	Blennid 2		4	0.06	0.2	7.0	4.8-10.0	Pr,Fl,Po	N	+
	Blenniid 4		5	0.07	0.2	13.3	8.0-20.0	Po,Ju	D,N	
	Blenniid 6		5	0.07	0.2	7.0	3.0-19.0	Pr,Po	D,N	
Tripterygiidae	Tripterygiid 1	4	281	3.30	9.3	5.7	3.4-15.2	Pr,Fl,Po	D**,N*	
Gobiidae	Gobiid 3		1	0.01	<0.1	15.0		Po	D	
	Gobiid 5		4	0.05	0.1	7.6	7.0-9.0	Po	D,N	
	Gobiid 7		13	0.17	0.5	13.2	10.0-17.0	Po	D,N	
	Gobiid 8		15	0.19	0.5	14.8	11.2-19.0	Po,Ju	D,N	
	Gobiid 9		11	0.14	0.4	8.9	2.5-13.8	Pr,Fl,Po	D,N	
Scombridae	Scombrid 2	12	57	0.87	2.5	2.9	2.2-3.5	Pr	D*,N	
Soleidae	Soleid 1		8	0.09	0.3	4.4	4.0-5.0	Po	D,N	

Total number = 2931
Total number of taxa = 88
Total number of families = 47

[A] Wallace (1975a,b); Wallace and van der Elst (1975); Whitfield (1980)
B < 0.2% of total catch listed in Appendix IV

In the 12-month study, stepwise regression analyses for each estuarine-association group showed that different environmental variables were important in accounting for the variability in fish densities and that it is species-specific (Table 8.2). Turbidity accounted for only 4% of the variation in densities of estuarine-dependent taxa whereas for partially estuarine-dependent taxa turbidity accounted for 9%. Temperature was the dominant factor for two of the abundant partially estuarine-dependent taxa, *Ambassis* sp. and *C.chanos*, each contributing 15% and 29% in the regression equations, respectively. Salinity was only significant for the estuarine-dependent species *R.holubi* accounting for 8% of variations in larval density ($P < 0.001$). Larval densities of Tripteygiid 1, a reef-associated species independent of estuaries, were not significantly correlated to any of the environmental variables (Table 8.2). With the data from the 24-h study included in the model, turbidity and temperature were dominant factors accounting for over 50% in most of the models (Table 8.2). Turbidity alone was the dominant factor for taxa partially dependent on estuaries, contributing to 53% in the regression equation. Estuarine-independent taxa were the least correlated to environmental variables with turbidity and temperature accounting for 26% of the variance in the model.

Table 8.2. Stepwise regression statistics of fish densities versus environmental variables (sa, salinity;te,temperature; tu, turbidity) for each estuarine-association group and the most abundant species in each group.

(adj, adjusted; R^2, coefficient of determination; ; R, correlation coefficient; F, F statistic; significance level = 0.05)

Estuarine-association group	12-month study				12-month + 24-h study			
	$_{adj}R^2$	R	F	significant variable	$_{adj}R^2$	R	F	significant variable
All taxa	0.04	0.20	7.27*	tu**	0.48	0.69	77.4***	tu***;-te*
Estuarine-dependent	0.04	0.20	6.59*	tu*	0.50	0.71	81.73***	tu***; -te*
Rhabdosargus holubi	0.08	0.28	13.32***	-sa***	0.10	0.32	9.65***	-sa***;tu*
Elops machnata	0.09	0.30	14.98***	tu***	0.52	0.72	179.22***	tu***
Thryssa vitrirostris					0.56	0.75	104.30***	tu***;-te*
Partially estuarine-dependent	0.09	0.30	14.95***	tu***	0.53	0.73	190.81***	tu***
Ambassis sp.	0.15	0.39	26.56***	te***	0.57	0.75	219.68***	tu***
Chanos chanos	0.29	0.54	58.82***	te***	0.54	0.73	97.55***	tu***;te*
Croilia mossambica	0.03	0.17	5.15*	tu*	0.56	0.75	104.77***	tu***;-te*
Non-estuarine					0.26	0.51	29.48**	tu***;-te**
Pomadasys olivaceum	0.05	0.22	8.21*	tu*	0.08	0.28	15.92***	tu***
Tripterygiid 1								

*P < 0.05; **P < 0.01; ***P < 0.001

8.2.3 Temporal and Spatial Trends in Fish Density

Three peaks in fish abundance occurred throughout the study period as a result of the seasonality of each estuarine-association group (Figure 8.3). Mean fish density was highest in November with 175 fish per $100m^3$ being recorded in the night catches (Figure 8.3A). This peak in abundance was due to larvae and juveniles of species independent of estuaries, in particular *P.olivaceum*, being present in November (Figures 8.3D and 8.4). The peak in abundance in August was due to an abundance of estuarine-dependent species (also at night - 68 fish per $100m^3$ - see Figure 8.3B) particularly sparids (*R.holubi* and *R.sarba*) and a mugilid (Figure 8.4). For partially estuarine-dependent species, larvae were most abundant in April (72 larvae per $100m^3$) and August (47 larvae per $100m^3$) due to the presence of *Ambassis* sp. and *D.sargus capensis*, respectively (Figures 8.3C and 8.4).

No significant differences in temperature or salinity were found between stations but turbidity was significantly higher at station 1 ($P = 0.001$, $F = 5.09$) (Figure 8.5). Mean fish densities of estuarine-dependent and partially estuarine-dependent taxa were significantly higher at stations 2 and 3 than at stations 4, 5 and 6 (Figure 8.5). Mean densities of all estuarine-association groups and turbidity were lowest at the station furthest from the estuary mouth i.e. station 6. Although the densities of estuarine-independent taxa were highest at station 2 this was not significant ($P > 0.05$).

The mean densities of all taxa together and for each estuarine-association group were significantly higher in night catches than in day catches ($P < 0.001$, 3-way ANOVAs, Table 8.3). Although station and month were also significantly different in terms of changes in fish densities, the day/night values were significantly higher than those for both station and month (Table 8.3). For individual abundant species in each group only *R.holubi* and *C. mossambica* had significantly higher densities at night ($P = 0.05$ and $P = 0.01$, respectively). Densities of the estuarine-dependent and partially dependent fish groups were significantly higher at stations 2 and 3 ($P < 0.01$ and $P < 0.001$, respectively). In contrast, densities of fish species independent of estuaries showed no significant trends with station ($P > 0.05$). The monthly changes in densities of the most abundant species were all significant whereas for all these species, no significant changes in densities were noted between stations ($P > 0.05$, Table 8.3). The

time x station interaction was only significant for *E.machnata* ($P < 0.05$) while the time x month interaction was significant for six of the eight abundant species, in particular *C.chanos* and Tripterygiid 1 ($P < 0.001$). Only the estuarine-dependent group was significant for the station by month interaction ($P < 0.05$).

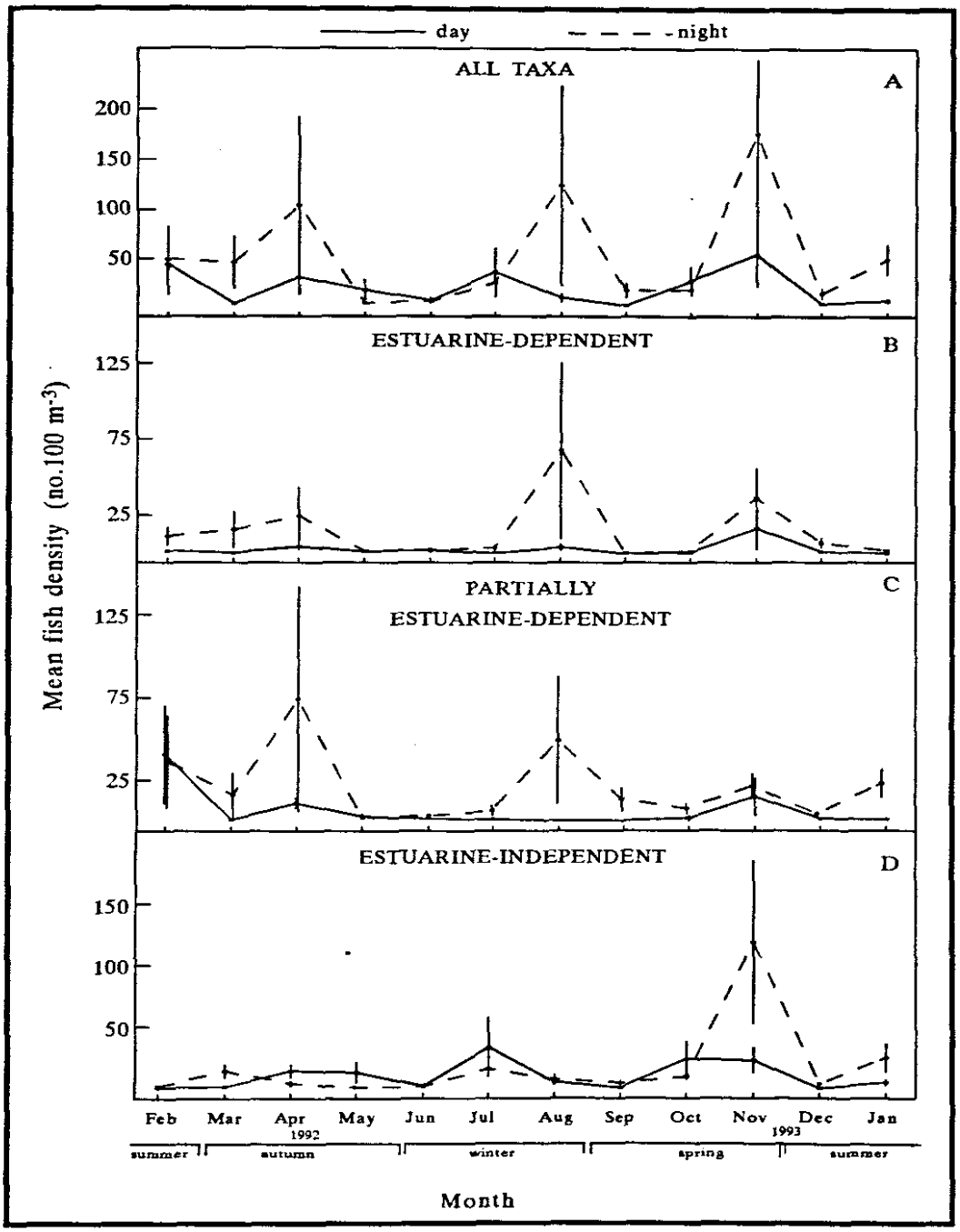


Figure 8.3. Mean monthly variations in larval and juvenile fish densities (± 1SE), in day and night catches, for all taxa together (A), estuarine-dependent taxa (B), partially estuarine-dependent taxa (C) and estuarine-independent taxa (D).

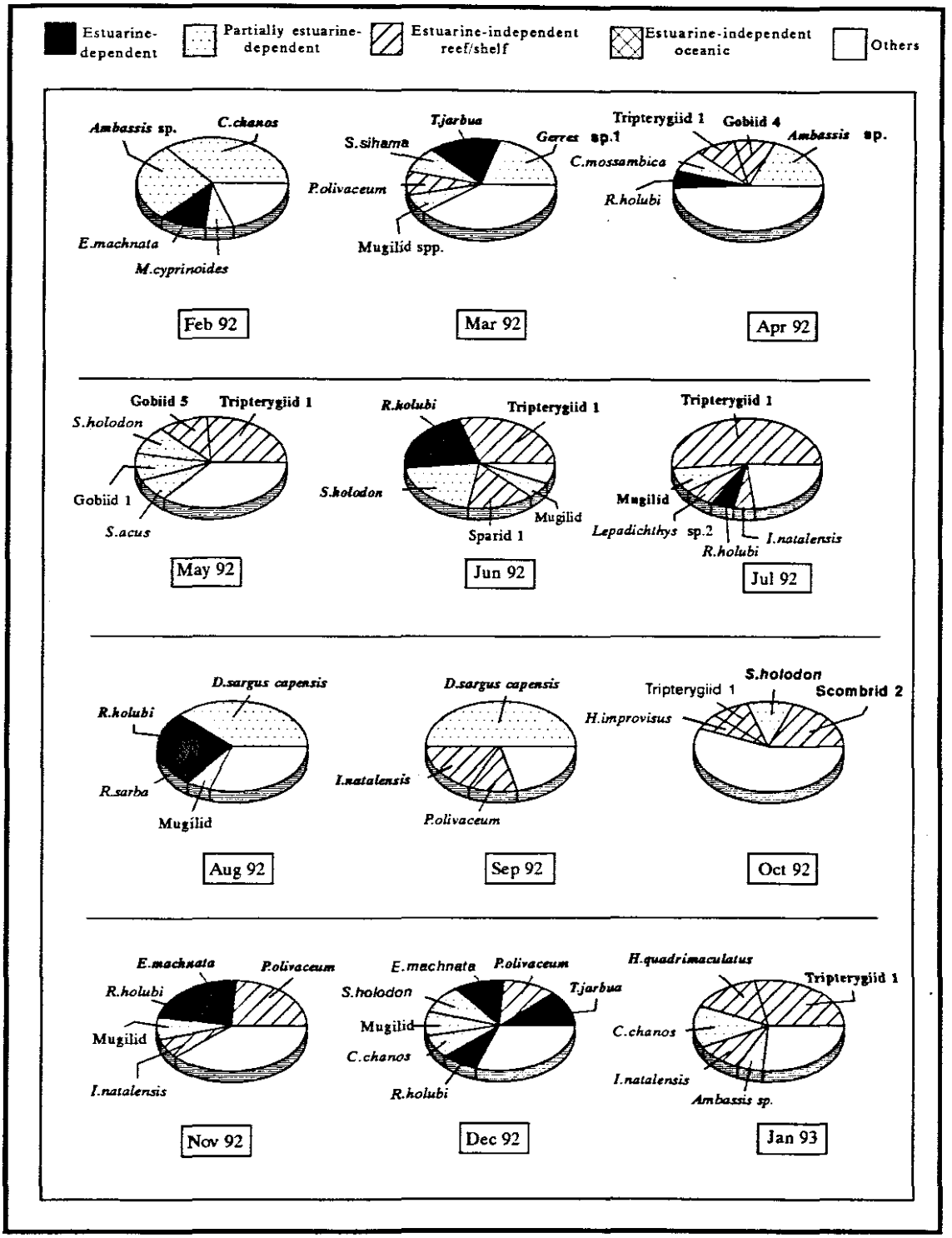


Figure 8.4. Percentage contribution of the most abundant species in the total catch sampled each month in the surf zone adjacent to the St Lucia Estuary.

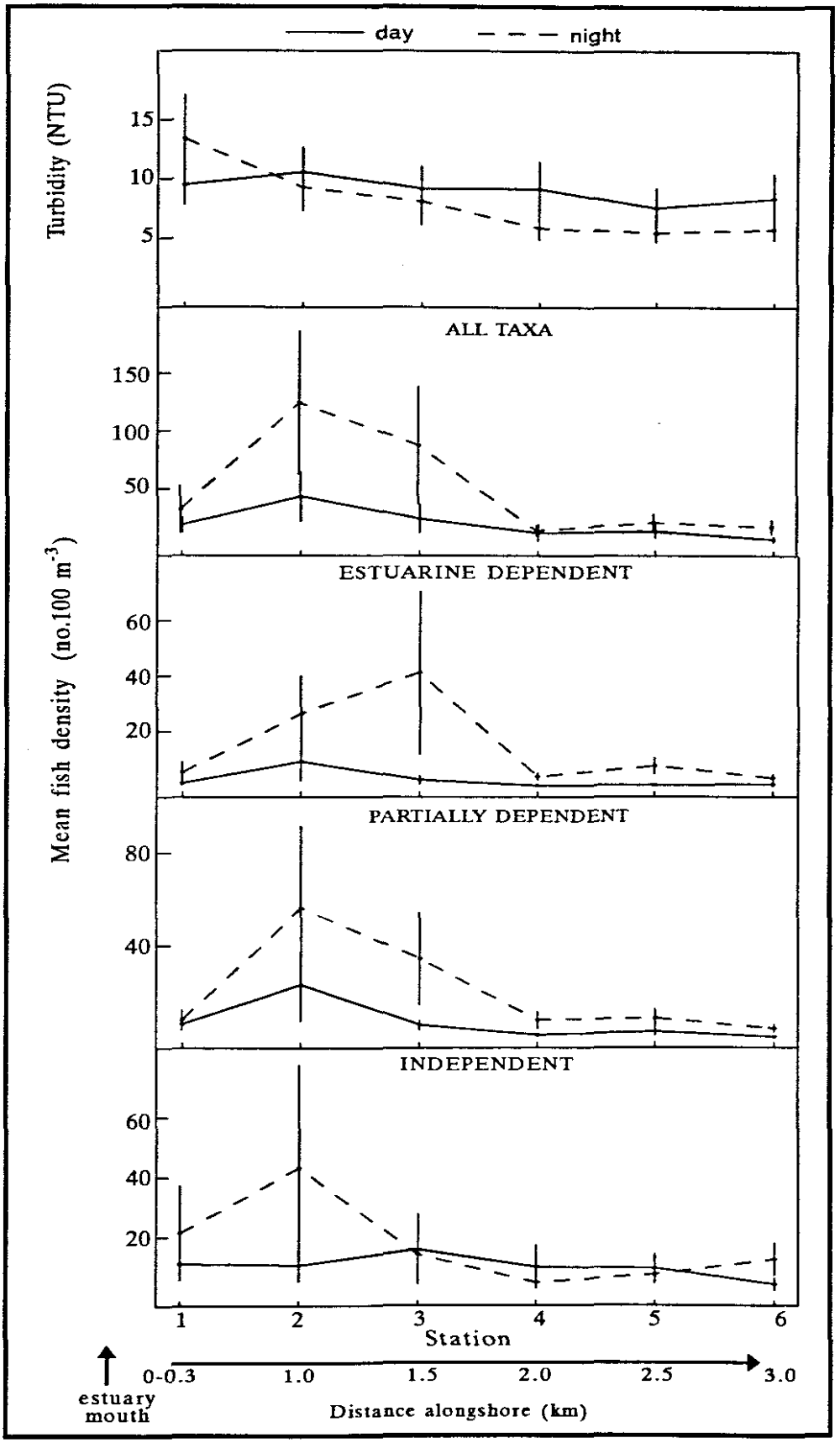


Figure 8.5. Spatial changes in turbidity and fish density of each estuarine-association group (± 1SE).

Table 8.3. Mean squares and significance levels for three-way ANOVA of densities of the most abundant species in each estuarine-association group. (DF=degrees of freedom).

Estuarine-association group	Main effects			2-way interaction		
	Time (D/N)[A] (DF=1)	Station (1 to 6)[B] (DF=5)	Month (1 to 12)[C] (DF=11)	Time x Station (DF=5)	Time x Month (DF=11)	Station x Month (DF=55)
All taxa	4.66*** (N>D)	0.82** (stn 2)	0.93***	0.11	0.42	0.27
Estuarine-dependent	6.56*** (N>D)	0.56** (stns 2,3)	0.91***	0.19	0.15	0.23*
Rhabdosargus holubi	0.65*	0.03	0.94***	0.18	0.29*	0.13
Elops machnata	0.05	0.06	0.69***	0.27*	0.04	0.06
Thyrssa vitrirostris	0.06	0.05	0.01	0.01	0.00	0.01
Partially estuarine-dependent	4.52*** (N>D)	1.13*** (stns 2,3)	0.81***	0.27	0.48*	0.32
Ambassis sp.	0.02	0.06	0.39**	0.21	0.25	0.08
Chanos chanos	0.02	0.10	0.80***	0.09	0.32***	0.07
Croilia mossambica	0.90** (N>D)	0.10	0.17***	0.01	0.04	0.04
Estuarine-independent	1.36* (N>D)	0.26	1.30***	0.17	0.64*	0.24
Pomadasys olivaceum	0.04	0.10	1.15***	0.21	0.31*	0.08
Tripterygiid 1	0.11	0.18	0.59***	0.25	0.65***	0.17

*p < 0.05; **p < 0.01; ***p < 0.001

[A] includes data from 24-h study. D, day; N, night

[B] stations where densites highest is indicated in parentheses and Fig 8.5.

[C] months where densities highest is indicated in Fig. 8.3.

8.2.4 24-h Study

A total of 13 731 larvae and juveniles, representing 43 taxa and 22 families, was collected in the 24-h study in February 1993 (Table 8.4) when the estuary mouth was closed. The most abundant species were *Ambassis* sp., *C.mossambica* and *C.chanos* each contributing 29.5%, 21.0% and 11.5% of the total catch, respectively. Other species contributing between 5 - 10% were *E.machnata*, *T.vitrirostris* and *Thryssa.setirostris*. Note that no sparid species were collected during this 24-h study but that during the 12-month study, the three sparid species, *R.holubi*, *D.sargus capensis* and *A.berda* were relatively abundant (see Table 8.1).

Over the 24-h period salinity values remained at 35.0, whereas temperature and turbidity values were lower at night (Figure 8.6). Turbidity reached a maximum of 709 NTU and a minimum of 50 NTU. In contrast, mean fish density was higher at night and reached a maximum of 5 853 larvae per $100m^3$ at 01h00. The lowest density of fish recorded was 287 larvae $100m^3$ during the day at 09h00. Note that both turbidity and fish density values were considerably higher than in all the previous months sampled of the 12-month study (Figures 8.3, 8.1 and Figure 8.6). This resulted in highly significant correlation coefficients with turbidity accounting for a large proportion of the variation in fish density (Table 8.2). Since no samples could be taken during high tides, tidal cycles could not be detected.

Table 8.4. Total catch, body length and developmental stage for all larval and juvenile fish taxa collected in the 24-h study in the surf zone adjacent to the St Lucia Estuary mouth (Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile; D, day; N, night - *abundant; **very abundant)

Family	Species	Rank overall	Total catch number	Total catch mean no.100m^{-3}	%	Body length (mm) mean	Body length (mm) range	Developmental stage	Presence
ESTUARINE-DEPENDENT									
Estuarine residents									
Gobiidae	*Psammogobius knysnaensis*		2	0.29	<0.1	6.5		Po	N
Eleotridae	*Redigobius* sp.		1	0.14	<0.1	6.0		Po	N
	Taenioides jacksoni	6	641	101.86	4.9	9.6	9.0-12.0	Po	D,N**
	Eleotrid 2		44	6.53	0.3	15.0	13.0-16.0	Po	D,N*
	Eleotrid 4		9	1.31	0.1	16.9	11.0-19.0	Po,Ju	D,N
Marine spawners dependent on estuaries									
Elopidae	*Elops machnata*	4	1102	152.74	7.4	28.7	19.0-39.0	Le	D**,N**
Engraulidae	*Thryssa vitrirostris*	5	982	139.25	6.7	19.7	11.5-32.0	Po,Ju	D*,N**
Teraponidae	*Terapon jarbua*		68	9.05	0.4	10.5	9.0-15.0	Po	D*,N*
Haemulidae	*Pomadasys commersonnii*		5	0.74	<0.1	9.5	8.2-10.5	Po	N
Monodactylidae	*Monodactylus argenteus*		35	4.94	0.2	5.4	4.8-6.5	Po	D,N
PARTIALLY ESTUARINE-DEPENDENT									
Catadromous									
Megalopidae	*Megalops cyprinoides*	9	543	76.73	3.7	22.6	18.0-33.0	Le	D*,N**
Freshwater and estuarine spawners									
Gobiidae	*Glossogobius callidus*		1	0.15	<0.1	9.2		Po	N
Estuarine and marine spawners									
Ambassidae	*Ambassis gymnocephalus*		1	0.13	<0.1	43.0		Ju	D
	Ambassis sp.	1	3975	608.73	29.5	5.6	3.2-8.0	Fl,Po	D*,N**
Gobiidae	*Croilia mossambica*	2	2698	433.02	21.0	11.0	7.0-12.7	Po	D*,N**
	Gobiid 1	8	485	78.52	3.8	5.6	4.0-7.0	Po	D,N**
	Taenioides esquivel	7	58	9.72	0.5	10.4	9.5-12.0	Po	D,N*
Marine spawners with juveniles abundant in estuaries									
Mugilidae	Mugilid spp.		5	0.80	<0.1	17.2	8.5-20.0	Po,Ju	N
Soleidae	*Solea bleekeri*		11	1.77	0.1	4.1	3.5-4.5	Fl,Po	N
Marine spawners with juveniles abundant at sea and in estuaries									
Engraulidae	*Stolephorus holodon*		5	0.71	<0.1	19.7	16.0-24.5	Po	D,N
Chanidae	*Chanos chanos*	3	1601	238.43	11.5	11.6	10.0-14.0	Po	D*,N**
Platycephalidae	*Platycephalus indicus*		1	0.14	<0.1	7.0		Po	D

cont.

Table 8.4 cont.

Haemulidae	*Pomadasys kakaan*		3	0.35	<0.1	10.4	10.0-11.2	Po	D,N
Leiognathidae	*Leiognathus equula*	10	281	39.60	1.9	11.4	8.0-30.0	Po,Ju	D*,N**
Gerreidae	*Gerres* sp1		86	12.04	0.6	8.7	6.0-15.0	Po	D*,N*
Sillaginidae	*Sillago sihima*		2	0.31	<0.1	13.0		Po	N
Lutjanidae	*Lutjanus argetimaculatus*		3	0.43	<0.1	14.8	14.5-15.0	Po	D
Sphyraenidae	*Sphyraena jello*		2	0.30	<0.1	19.0	18.0-20.0	Po	N
ESTUARINE-INDEPENDENT									
Reef and shore taxa									
Engraulidae	*Thryssa setirostris*	6	876	118.94	5.8	27.3	22.0-51.0	Po,Ju	D**,N**
Notocheiridae	*Iso natalensis*		1	0.15	<0.1	5.5		Pr	N
Haemulidae	*Pomadasys olivaceum*		57	7.15	0.3	19.6	10.8-29.0	Po,Ju	D*,N
Leiognathidae	*Secutor insidiator*		1	0.21	<0.1	27.0		Ju	N
Carangidae	*Trachinotus* sp.1		9	0.48	<0.1	15.3	13.0-16.0	Po	D
Scaridae	*Scarus* sp.		2	0.30	<0.1	8.8	8.5-9.0	Po	N
Polynemidae	*Polydactylus plebeius*		2	0.29	<0.1	48.5	42.0-55.0	Ju	N
Trichonotidae	*Trichonotus marleyi*		1	0.15	<0.1	15.0		Po	D
Blenniidae	*Istiblennius* sp.		1	0.13	<0.1	15.0		Po	D
Gobiidae	Gobiid 5		23	3.77	0.2	11.0	10.0-12.0	Po	D,N*
	Gobiid 7		92	14.12	0.7	13.6	13.0-14.5	Po	D,N*
	Gobiid 8		10	1.59	0.1	10.4	9.5-13.0	Po	D,N
	Gobiid 9		4	0.56	<0.1	3.9	3.5-4.2	Po	N
	Gobiid 11		1	0.14	<0.1	5.5		Po	N
	Gobiid 12		1	0.14	<0.1	10.0		Po	N

Total number = 13731
Total number taxa = 43
Total number families = 22

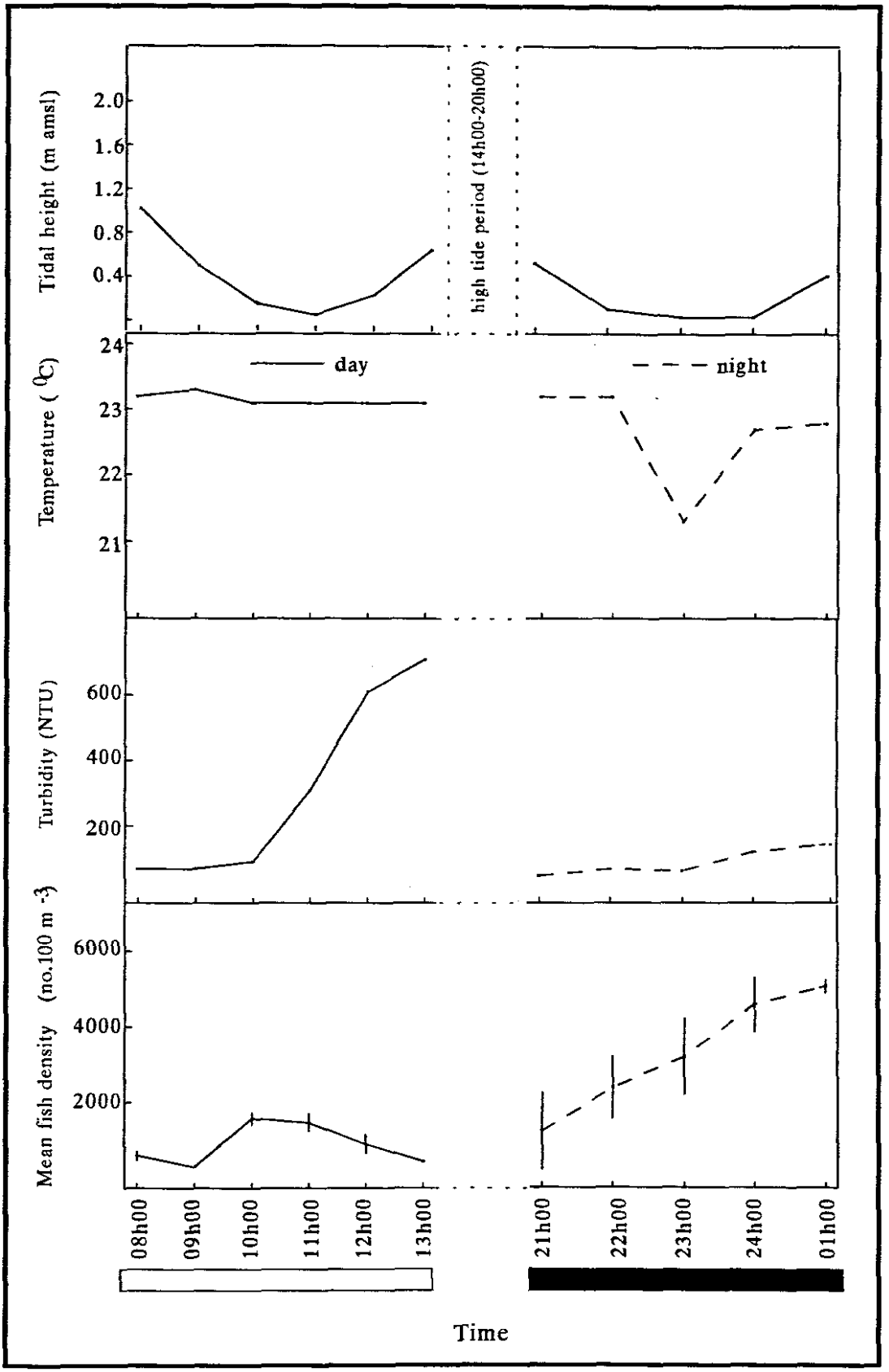


Figure 8.6. Diel changes in tidal height (meters above mean sea level), temperature, turbidity and mean (of replicate samples) fish density during the 24-h study.

8.2.5 Developmental Stages

Developmental stages were predominantly postflexion (old larvae) in the estuarine-associated categories for both the 12-month and 24-h study, excluding leptocephali larvae in the catadromous category (Figure 8.7). In the 12-month study, approximately 29% of larval stages of estuarine-independent taxa were young larvae (preflexion and flexion). However, during the 24-h study 50% of the fish in the estuarine-independent category were juveniles. This was because many juvenile *T.setirostris* and *P.olivaceum* were collected during the 24-h study (Table 8.4). Leptocephali larvae were present in both the 12-month and 24-h study since the estuarine-dependent species *E.machnata* and the catadromous species *M.cyprinoides* were present in both studies (see Tables 8.1 and 8.4).

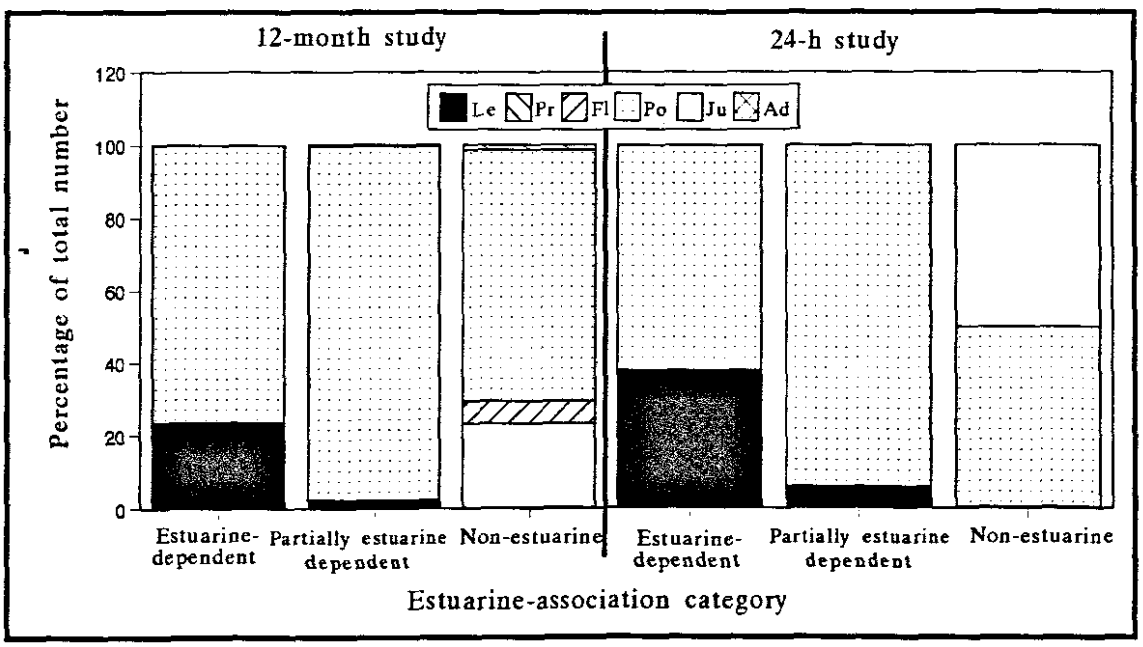


Figure 8.7. Percentage contribution of the different developmental stages for each estuarine-association group in the 12-month and 24-h studies. (Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile).

In the 12-month study, postflexion larval stages were dominant in most months sampled, except May, July and October when preflexion larval stages were prevalent (Figure 8.8). Leptocephali were most abundant in November and December. A few juveniles were present in most months except from May to July

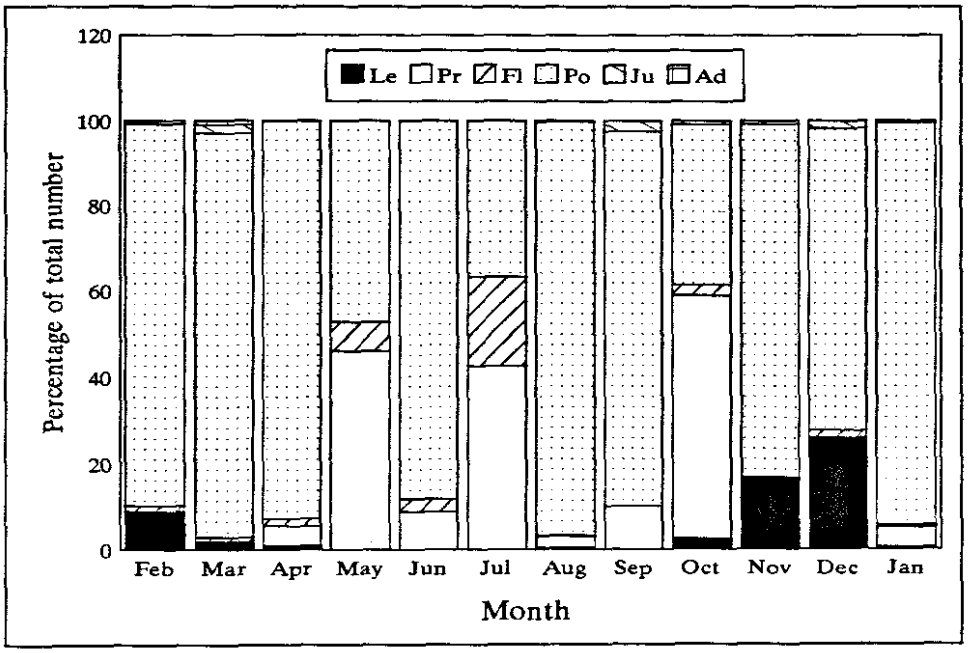


Figure 8.8. Monthly percentage composition of developmental stages of all fish sampled in the study. Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile

8.2.6 Estuarine-Association

In the 12-month study, the majority of larvae and juveniles were those of estuarine-independent species which comprised 54% (49 taxa in total - see Table 8.1 and Appendix IV) of all taxa and 38% of total density (Figure 8.9A). Estuarine-dependent species were least abundant (25% of total density), whilst partially estuarine-dependent taxa comprised the remaining 36%. Eleven estuarine-dependent and 17 partially estuarine-dependent species were recorded during the 12-month study period (Figure 8.9A and Table 8.1).

In the 24-h study, estuarine-dependent and partially estuarine-dependent taxa were particularly abundant and comprised 93% of the total density (Figure 8.9B). The contribution to partially estuarine-depndent taxa was mainly due to *Ambassis* sp. and *C.mossambica* which were first and second overall in abundance (Table 8.4). Of the estuarine-associated taxa, 10 species were estuarine-dependent and 19 species were partially estuarine-dependent (see Table 8.4). .

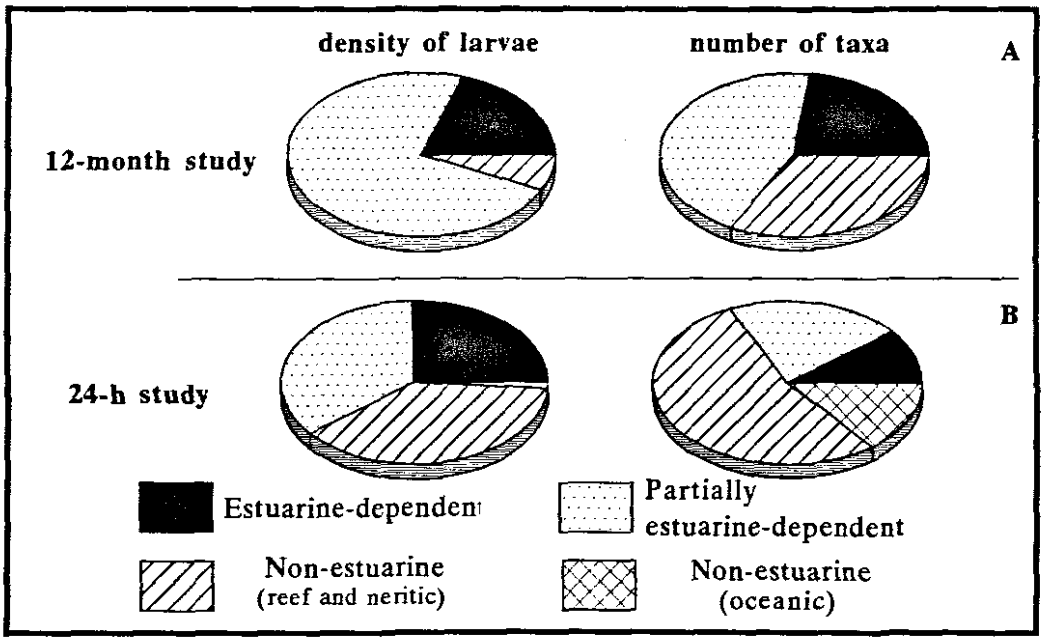


Figure 8.9. Percentage composition of all developmental stages in the 12-month (A) and 24-h study (B).

8.3 Discussion

8.3.1 Composition of Larval and Juvenile Fish Assemblage

The larval and juvenile fish assemblage in the surf zone adjacent to the St Lucia Estuary was considerably more diverse (88 taxa) than that found in the surf zone off the Swartvlei Estuary (26 taxa; Whitfield 1989c). Several of the families of larval and juvenile fish found in surf zone habitats of the Eastern Cape (Lasiak 1981; Bennett 1989b; Whitfield 1989c; Clark *et al.* 1994) were also found in the present surf zone study off the St Lucia Estuary. Of particular note are *P.olivaceum*, *D.sargus capensis*, *R.holubi*, mugilid spp., *I.natalensis*, *Monodactylus* spp. and *Solea bleekeri*. Since St Lucia is in a subtropical region, other more tropical species not found in the temperate Eastern Cape studies were abundant in the present study, particularly *C.chanos*, *E.machnata*, *Ambassis* sp., *Thryssa* spp. and *C.mossambica*. *C.chanos* larvae are particularly abundant in the surf zone in the tropical waters of Japan (Senta and Kinoshita 1985; Morioka *et al.* 1993) and are known to spawn in offshore waters (Leis and Reader 1991) and to move to inshore nursery areas as they develop (Morioka *et al.* 1993).

Tripterygiids are reef-associated fish species abundant in coral atoll lagoons (Leis 1991) and are most abundant in warm waters (Smith and Heemstra 1986). In KwaZulu-Natal, larval and juvenile tripterygiids were recorded in abundance at a site adjacent to a rocky reef inside the mouth of the Kosi Estuary (Harris *et al.* 1995 - see Addendum), in the St Lucia Estuary (Table 6.1, Chapter 6) and in tidal pools (Beckley 1994). Trypterygiid 1 was also relatively abundant in six of the 12 months of the present surf zone study (Figure 8.4). It is interesting to note the presence of a few schindleriids in the surf zone since these fish have not been previously recorded in southern Africa (Smith and Heemstra 1986). Schindleriids were also relatively abundant in the mouth of the Kosi Estuary (Harris and Cyrus 1995c - see Addendum) which is approximately 150 km north of St Lucia Estuary.

8.3.2 Environmental Conditions Affecting Fish Abundance

Several environmental variables (current, temperature, salinity, turbidity, olfactory cues) are responsible for eliciting a response in larval fish recruitment to estuarine nursery areas (Boehlert and Mundy 1988). The surf zone current along the KwaZulu-Natal coast is predominantly in a northerly direction (Begg 1978; Rossouw 1984) but a southerly longshore drift does occur in the surf zone when northerly winds blow (Wright 1990). Although the surf zone current is predominantly north flowing it is also likely that recruiting fish larvae could originate from the Agulhas Current, the prominent south flowing current along the east coast of South Africa (Schumann 1987), which is significant in the dispersal of planktonic eggs and larvae (Heydorn 1978a). The current is characterised by Indian Ocean subtropical surface water and shoreward intrusions of Agulhas Current water have been recorded consistently (Beckley and Van Ballegooyen 1992). Recruiting fish larvae would also originate from the nearshore reefs in the region. Recruiting fish larvae entering the surf zone near the St Lucia Estuary mouth are predominantly postflexion larvae and are thus capable of active swimming behaviour. Fish larvae of certain species can behaviourally alter their position relative to currents and are thus more active plankters than was previously thought (Leis 1991). Whitfield (1989c) observed old larvae maintaining their position in the inner surf zone near the mouth of the Swartvlei Estuary. Results of the present study indicate that in the St Lucia region, the larvae and juveniles of marine fish species which are dependent on estuaries to some degree, accumulate near the mouth of the St Lucia Estuary (Figure 8.5) and would subsequently utilise flood tidal currents to facilitate their entry into the estuarine environment.

Turbidity is one of the most important factors affecting fish distribution in southern African estuaries (Blaber 1987; Cyrus 1992) and nearshore/shallow-water marine environments (Abou-Seedo *et al.* 1990). Martin *et al.* (1992) found that elevated turbidities associated with flooding of the St Lucia Estuary clearly contributed to increased recruitment densities of larval and juvenile fishes into the estuary. Turbidity, in combination with other environmental variables, was a dominant factor affecting larval densities in the St Lucia Estuary (Table 6.2, Chapter 6). The present study showed that both temperature and turbidity play a significant role in affecting fish densities

(Table 8.2). Whitfield (1994c), however, found that turbidity *per se* may not be an important factor in recruitment of larval and 0+ juvenile fish into three Eastern Cape estuaries. He suggested that olfactory cues entering the marine environment from estuaries may be more important in guiding immigrating fish into these systems and that the magnitude of olfactory cues entering the nearshore marine zone will decrease with decreasing axial salinity gradient within an estuary. In the surf zone study by Whitfield (1989c) temperature was correlated to ichthyoplankton densities. Modde and Ross (1981) found that the dominant factors affecting the abundance of fishes in the surf zone of Horn Island were tide level, time of day and temperature. It, therefore, seems that fish abundance in the surf zone is influenced by locality and on what factors are most important in eliciting a recruitment response in different fish species .

8.3.3 Temporal and Spatial Trends in Fish Abundance

Results from statistical analyses (Tables 8.2 and 8.3), and temporal and spatial trends in fish abundance (Figures 8.3 and 8.5), indicated that much of the variability in fish abundance in the surf zone can be accounted for by changing environmental conditions on a temporal (seasonal and diel) and spatial (station) basis.

Although larval and juvenile fish occurring in surf zones generally peak in abundance in spring and summer, a second peak in abundance can also occur in winter (Modde and Ross 1981; Ruple 1984; Senta and Kinoshita 1985; Kinoshita 1986; Whitfield 1989c). This winter peak is generally due to the presence of sparid species such as *Sarpa salpa* (Whitfield 1989c), *R.sarba* (Kinoshita 1986, present study), *R.holubi, D.sargus capensis* and *R.sarba* (present study), but in the northern Gulf of Mexico this winter peak was due to a clupeid (*Brevoortia patronus*) and a sciaenid (*Leiostomus xanthurus,* Ruple 1984). Note that in the 24-h study, which was in summer, no sparid larvae were collected (Table 8.4) since the sparids *R.holubi, D.sargus capensis* and *R.sarba* are more abundant between late autumn, winter and spring (Wallace 1975b). In the present study, Tripterygiid 1 was also dominant in winter and Tricklebank *et al.* (1992) found that the winter peak in ichthyoplankton in the nearshore waters off New Zealand was primarily due to tripterygiids. A seasonal variation in dominant species occurred in the present study (Figure 8.4) and also in the studies of Modde and Ross

(1981) and Ruple (1984) in the surf zone of the northern Gulf of Mexico. The present study indicated that this variation was a result of different seasonal trends for the different estuarine-association categories. Estuarine and marine species with some degree of dependence on estuaries were most abundant in the surf zone near the St Lucia Estuary mouth in mid autumn, late winter and late spring. Larval densities in the St Lucia Estuary similarly peaked in autumn and late spring, but not in winter (see Figure 6.4, Chapter 6). Recruitment of most juvenile fish species into Natal estuaries occurs during late autumn, winter and spring (Wallace 1975a,b) with many of these species having a prolonged recruitment period (Wallace and van der Elst 1975; Whitfield and Kok 1992).

Fish densities and turbidities both decreased with distance from the St Lucia Estuary mouth, except at station 1. Since the configuration of the St Lucia Estuary mouth changed considerably during the present study, the position of station 1 varied and sometimes was sampled in the mouth of the estuary on ebb tides. This would explain the lower densities of fish occurring at this site. Whitfield (1989c) found that larval densities were higher near the mouth of the Swartvlei Estuary prior to estuarine recruitment. When the Swartvlei Estuary mouth was closed, there was still a high concentration of larvae in the vicinity of the sand bar at the mouth which suggested that seepage of estuarine water through the sand bar acted as an olfactory cue to estuarine-associated species in the surf zone (Whitfield 1989). The St Lucia Estuary mouth was closed during the summer recruitment period (December to February) when the diel study was undertaken, and unusually high concentrations of estuarine-associated fish larvae (for example, *Ambassis* sp.- 477 larvae per $100m^3$) were sampled. Although there was only one station, these very high concentrations of larvae in the vicinity of the estuary mouth suggest that they had accumulated there waiting to recruit into the system. In this case, the cue may have also been olfactory.

Endogenous activity rhythms (daily, tidal and lunar periodicity) are important in recruitment to estuarine nursery areas (Boehlert and Mundy 1988). Ruple (1984) found that fish larval densities were significantly higher in night collections than day collections which was partly explained by gear avoidance of some larvae, especially larger engraulids caught at night. Our study also found significantly higher densities at night for both the monthly study ($p < 0.05$) and the diel study ($p < 0.01$) but that it was

species-specific (see Presence column in Tables 8.1 and 8.4). A significantly larger mean size of larvae caught in plankton nets at night suggests gear avoidance (Lyczkowski *et al.* 1990). Both this study and Whitfield (1989c), which used similar gear, did not find significantly larger larvae at night. In this study, mean size of three of the six most abundant species was not significantly different between day and night catches (ANOVA, $P > 0.05$). The other three abundant species (*T.vitrirostris, Ambassis* sp. and *P.olivaceum*) had a significantly larger mean size in the day catches (ANOVA, $P < 0.05$, $F = 5.38$; $P < 0.0001$, $F = 69.01$; $P < 0.0001$, $F = 84.83$, respectively). Whitfield (1989c) similarly found that the diel catches in fish larvae was species-specific but that densities were not significantly different between day and night catches. He also found that tidal phase was important in governing larval fish abundance with more larvae being present at low tide. In the study by Modde and Ross (1981) engraulids and clupeids (late larval and early juvenile) moved out of the surf zone during the day, whereas, carangids exhibited little change in daily abundance. They suggested that predator avoidance could be an important reason for this pattern. In contrast, Senta and Kinoshita (1985) found that larval fishes were more abundant during the day with no apparent influence of tidal cycle.

8.3.4 Size of Fish in Relation to Recruitment Strategies

The occurrence of newly hatched larvae or early developmental stages can be used as an indicator of time of spawning (Ruple 1984). The predominance of postflexion larvae in the surf zone of St Lucia indicates that the spawning of these marine species occurs in offshore waters sometime within one month prior to moving into the surf zone/nearshore and estuarine nursery areas. Daily growth rings in otoliths of *C.chanos* have shown that this species enters the surf zone habitat within 15 to 25 days after hatching and leaves after 10 days (Morioka *et al.* 1993). The larvae are generally in the same narrow size range of 10.0 - 17.0 mm SL (mean 12.4 mm; Senta and Kinoshita 1985; Morioka *et al.* 1993). *C.chanos* larvae in the same size range were also found in the present study, both in the surf zone and in St Lucia Estuary (Table 6.1, Chapter 6). Only a few preflexion and flexion larval stages of estuarine-associated species (e.g. *R.sarba, S.holodon* - see Table 8.1) were collected which suggests that the spawning grounds of these species are

of close proximity. During a study in the nearshore marine environment of St Lucia (0.5 to 2.5 km offshore from the St Lucia Estuary mouth - Chapter 9) young larvae of *R.sarba* and *S.holodon*, in addition to other estuarine-associated species, were also found. However, old larvae of a number of estuarine-associated species were also prevalent indicating that only certain species have nearby spawning grounds. Ripe running and partially spawned specimens of *R.sarba* were recorded on the KwaZulu-Natal coast (Wallace and van der Elst 1975) indicating inshore spawning. Many small larvae of a sciaenid, *Bairdiella chrysoura* (< 4.0 mm) were found in the surf zone of the study by Ruple (1984). This species is known to spawn in estuarine and nearshore coastal waters (Ruple 1984).

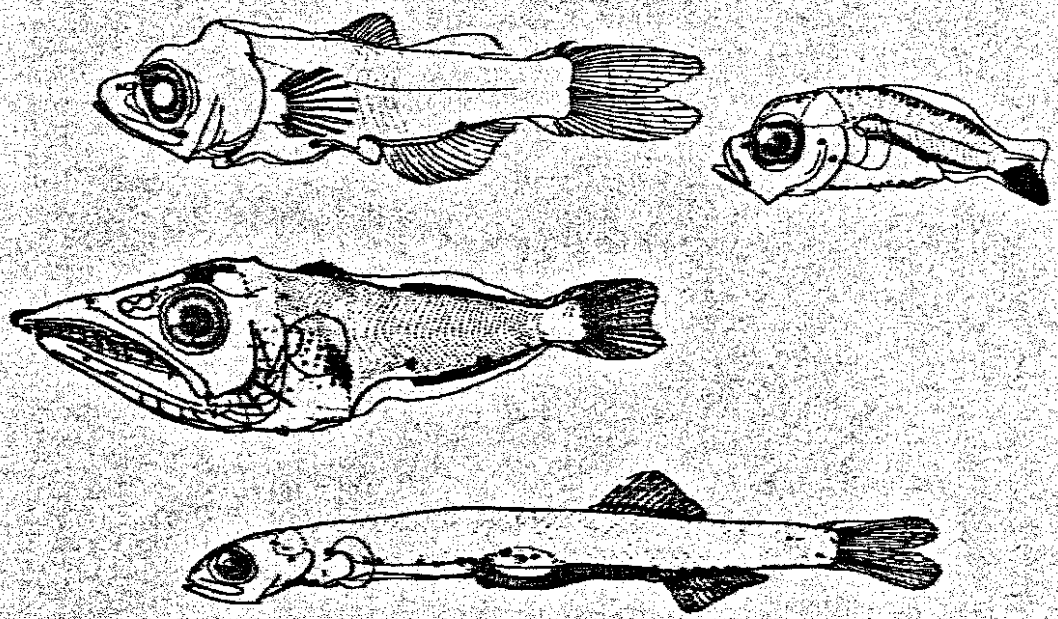
Restriction to a particular nursery area may be indicative of dependency on that habitat for survival (Lasiak 1981). A number of studies have shown that certain fish species at the juvenile stage are dependent on surf zones as nursery areas (Modde 1980; Lasiak 1981; Bennett 1989) which is indicated by the difference in species composition of the dominant species between the estuary and adjoining surf zone. Of the 29 estuarine-associated taxa recorded in the St Lucia surf zone 22 (73%) are common as juveniles or adults in the St Lucia Estuary (last column, Table 8.1). This suggests that the surf zone adjacent to the St Lucia Estuary serves a nursery function only for certain species. The degree to which larval fishes utilize the surf zone habitat varies depending on the species (Ruple 1984). Species which appear to be more dependent on surf zones during late larval stages are *T.setirostris*, *C.chanos*, *I.natalensis*, *P.olivaceum*, *D.sargus capensis* and Mugilid 1 since these species were more abundant in the surf zone than in the estuary (see Table 6.1). During the 24-h study, when the St Lucia Estuary mouth had been closed for two months, 15% of all taxa and four of the five most abundant species (*Ambassis* sp., *C.mossambica*, *E.machnata* and *T.vitrirostris*) collected were estuarine-dependent species and were present in particularly large numbers at the sandbar blocking the estuary mouth in anticipation of entering the St Lucia estuarine system. The latter four species were also abundant as postflexion larvae (and leptocephali for *E.machnata*) in the larval fish survey of the estuary (see Table 6.1).

8.3.5 Nursery Function of Surf Zone Habitat and Estuarine-Dependence

The occurrence of truly-estuarine species (category Ia), e.g. *G.aestuaria*, in the surf zone are probably stray individuals from the estuary. Whitfield (1989b) only recorded larval *G.aestuaria* after the Swartvlei Estuary mouth had opened and individuals got washed out on the flood tide. In the diel study, when the St Lucia Estuary mouth was closed, three goby species from category Ia were collected. They could have strayed from the Umfolozi River mouth approximately 1 km south of the St Lucia Estuary mouth (Figure 2.6, Chapter 6) but gobies in this category often have their larval stage completed in the marine environment (Whitfield 1994b) . The reef- and oceanic-associated taxa found as larvae in the St Lucia surf zone are also classified as strays. The presence of oceanic-associated fish larvae indicates that a shoreward intrusion of Agulhas Current surface water has occurred. Large concentrations of myctophid larvae often occur close inshore on the southeast coast of South Africa as a result of shoreward intrusions of Agulhas Current surface water (Olivar and Beckley 1994a).

CHAPTER 9

The Larval Fish Assemblage in the Nearshore Coastal Zone off the St Lucia Estuary Mouth



9. THE LARVAL FISH ASSEMBLAGE IN THE NEARSHORE COASTAL ZONE OFF THE ST LUCIA ESTUARY MOUTH

9.2 Introduction

The majority of fish species utilizing estuaries spawn at sea with the larval stages subsequently moving inshore and recruiting into estuarine nursery areas for the juvenile stage of their life cycle (Haedrich 1983; Miller *et al.* 1984; Norcross and Shaw 1984; Shaw *et al.* 1988). A number of ichthyoplankton studies have been undertaken in the nearshore coastal zone adjacent to estuaries to identify larvae of those fish species which are associated with and abundant in estuaries (Clark *et al.* 1969; Chenoweth 1973; Beckley 1985; Miskiewicz 1987; Shaw *et al.* 1988; Wang *et al.* 1991; Jennings and Pawson 1992; Tzeng and Wang 1993). For recruitment into estuaries, the first phase of movement of larval fish spawned offshore is the accumulation of larvae in the nearshore coastal zone (Boehlert and Mundy 1988) and they are typically transported by drift to the nearshore environment (Miller *et al.* 1984). Tzeng and Wang (1993) have shown that ontogenetic behavioural changes of fish larvae may play an important role in determining the abundance of the fish larvae in nearshore coastal waters. The position which fish larvae occupy in the water column and their ability to regulate this position in response to physical and/or chemical conditions, are important factors in the retention process (Weinstein *et al.* 1980). A number of studies have shown that vertical migration in coastal waters is an important behavioural mechanism influencing the landward transport and retention of estuarine-dependent species (Boehlert *et al.* 1985; Brewer and Kleppel 1986; Shaw *et al.* 1988; Lyczkowski-Shultz and Steen 1991; Norcross 1991).

The estuarine dependence of certain marine fish species has been questioned since many of the juveniles of these species also occur in the nearshore environment (Hedgpeth 1982; Haedrich 1983; Claridge *et al.* 1986). This is the case in south-western Australia since inshore marine waters are protected and provide suitable nursery habitats, but this is not the case in southern Africa (Potter *et al.* 1990). Conversely, the shallow coastal waters off southern California represent a nursery area for larval fishes (Barrett *et al* 1984). The southern African coastline, in particular KwaZulu-Natal, is exposed and has a high energy surf zone (Rossouw 1984). As a result, estuaries are the main source of nursery habitat in the region (Wallace *et al.* 1984; Cooper *et al.* 1995). The adjacent

coastal zone of KwaZulu-Natal is influenced considerably by the close proximity of the Agulhas Current because of a narrow continental shelf with a steep slope (Martin and Flemming 1988). The Agulhas Current is of tropical and subtropical origin and therefore transports larvae from the Indo-Pacific region to the southern African region (Heydorn 1978a; Schumann 1988). Beckley (1993) presented results indicating that oceanographic features, such as shoreward intrusions, associated with the shoreward edge of the Agulhas Current results in retention of linefish larvae on the shelf for southward dispersal to nursery areas. Current reversals and eddies inshore of the Agulhas Current are important in the transport and retention of larvae of estuarine-associated fishes in the KwaZulu-Natal region (Heydorn 1978a).

The majority of coastal ichthyoplankton studies on the south-eastern coast of South Africa have been undertaken in estuaries (Melville-Smith and Baird 1980; Melville-Smith 1981; Whitfield 1989a; Harrison and Whitfield 1990; Whitfield 1994c) but also in the surf zone (Whitfield 1989c). Only two studies on nearshore (< 4km offshore) ichthyoplankton have been undertaken (Beckley 1986; Tilney and Buxton 1994) and were restricted to the Eastern Cape. The aim of the study by Beckley (1986) was to investigate the availability of larvae to recruit into coastal nursery areas from the nearshore region of Algoa Bay. The larval fish assemblages in the St Lucia Estuary and in the adjacent surf zone showed that larvae of many marine fish species associated with estuaries in the region were present (Chapters 6 and 8). To understand how and from where from these marine-spawned larvae recruit to the St Lucia estuarine environment information on the nearshore larval fish assemblage is required. The present study investigates the composition, abundance and distribution of fish larvae in the nearshore coastal zone off the mouth of the St Lucia Estuary. Temporal and spatial patterns in environmental variables and larval abundance patterns of dominant species are assessed. In addition, possible mechanisms of larval transport and retention on the shelf and proximity of spawning grounds of estuarine associated species are discussed.

9.2. Results

9.2.1. Environmental Variables

During the period July 1990 to January 1991 mean monthly salinities in the nearshore coastal zone, off the St Lucia Estuary mouth (see Figure 2.7, Chapter 2), were essentially marine with a maximum of 36.0 ‰ in July and September 1990 (Figure 9.1), with mean salinities differing significantly between sampling dates ($F = 44.46$; $P < 0.0001$). Salinities declined from February to June 1991 with a minimum of 32 ‰ in June 1991. Top and bottom salinities were not significantly different ($F = 0.69$; $P = 0.53$) but did differ significantly between stations ($F = 4.30$; $P = 0.02$) with lower salinities at the stations closest to the shore (Figure 9.2).

Water temperature differed significantly between sampling periods ($F = 589.63$; $P < 0.0001$) and reached a maximum of 26.4°C in February 1991 and a minimum of 19.6°C in August 1991 (Figure 9.1). Temperature values were significantly higher in top samples ($F = 49.66$; $p < 0.0001$) and at station 5 which is furthest offshore ($F = 8.28$; $p < 0.0001$; Figure 9.2).

Water turbidity showed the greatest variations from January to June 1991 with two peaks occurring in January and March (Figure 9.1). The minimum mean turbidity was 1 NTU in September 1990 and the maximum mean turbidity was 84 NTU in March 1991. Note that the peaks in turbidity were predominantly in bottom samples and were significantly higher than in top samples ($F = 62.84$; $p < 0.0001$). Water turbidity was significantly higher at stations 2 and 3 ($F = 4.63$; $p = 0.0002$) than at the stations close to shore (stations 1, 6 and 7) and those furthest offshore (stations 4 and 5) (Figure 9.2).

The Temperature-Salinity plot (Figure 9.3) shows that during the study period the nearshore waters off the St Lucia Estuary mouth were characterised by three water masses (adapted from Schumann 1988):

- tropical surface water (TSW) which has higher temperatures and salinities,
- subtropical surface water (STSW) with lower temperatures but still marine,
- river outflow (ROF) - this water mass has lower salinities and low to high temperatures because of high rainfall in certain months which results in increased river outflow.

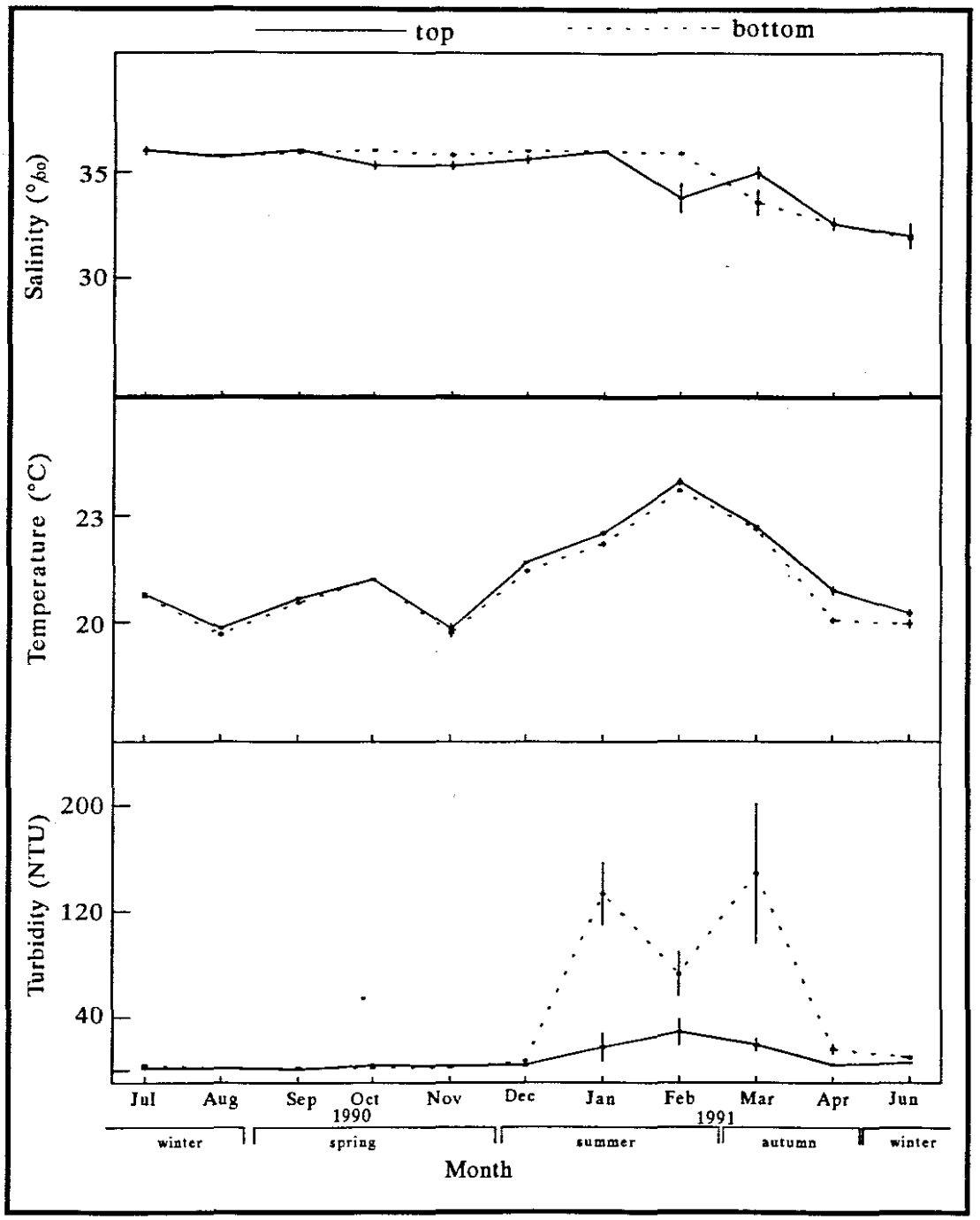


Figure 9.1. Mean monthly variations (± 1SE) of the environmental variables (salinity, temperature and turbidity) for top and bottom samples in the nearshore coastal zone off the St Lucia Estuary mouth, for the study period.

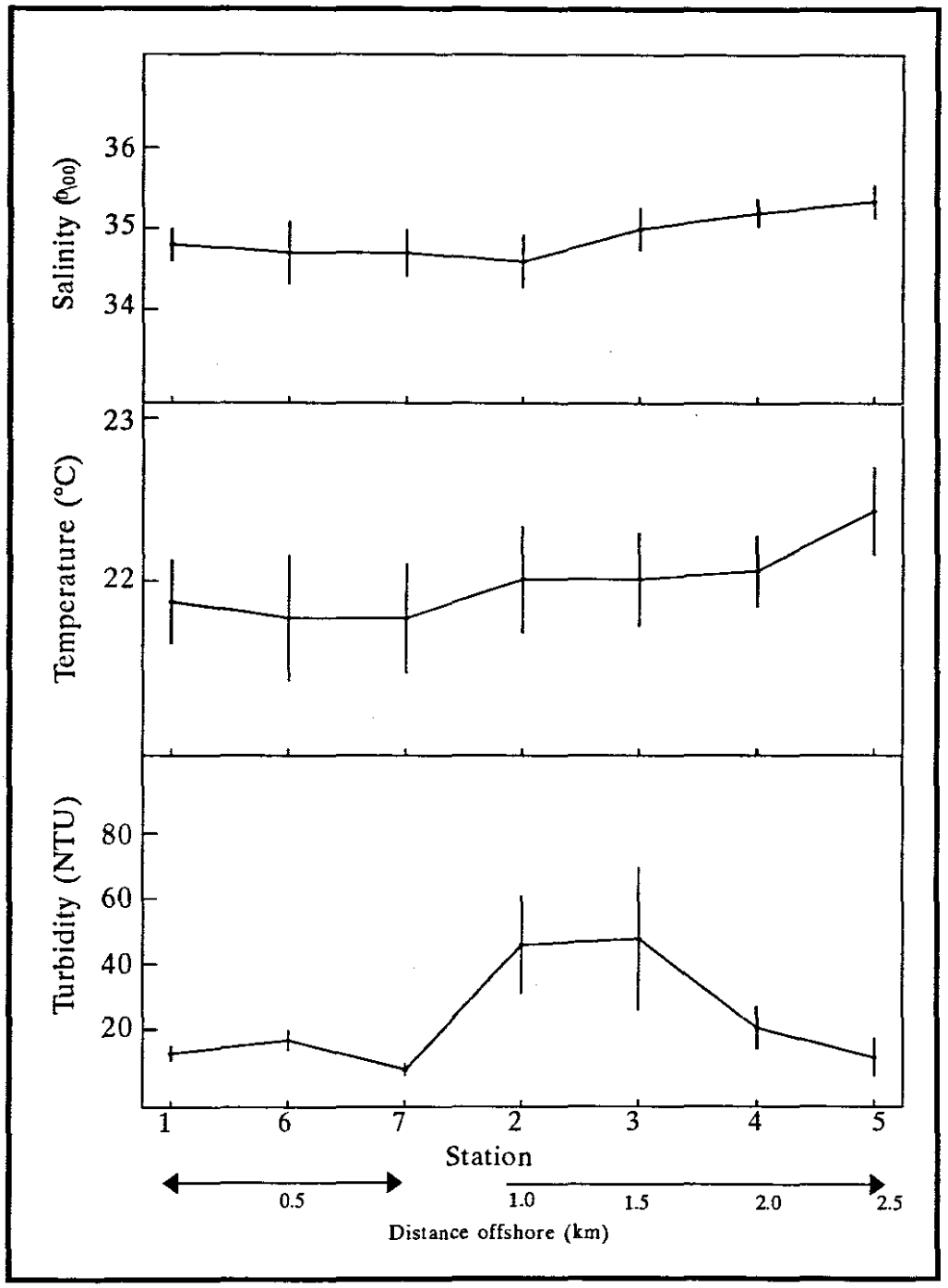


Figure 9.2. Mean variations (± 1SE) of the environmental variables (salinity, temperature and turbidity) at each station along the transect in the nearshore coastal zone off the St Lucia Estuary mouth, for the study period.

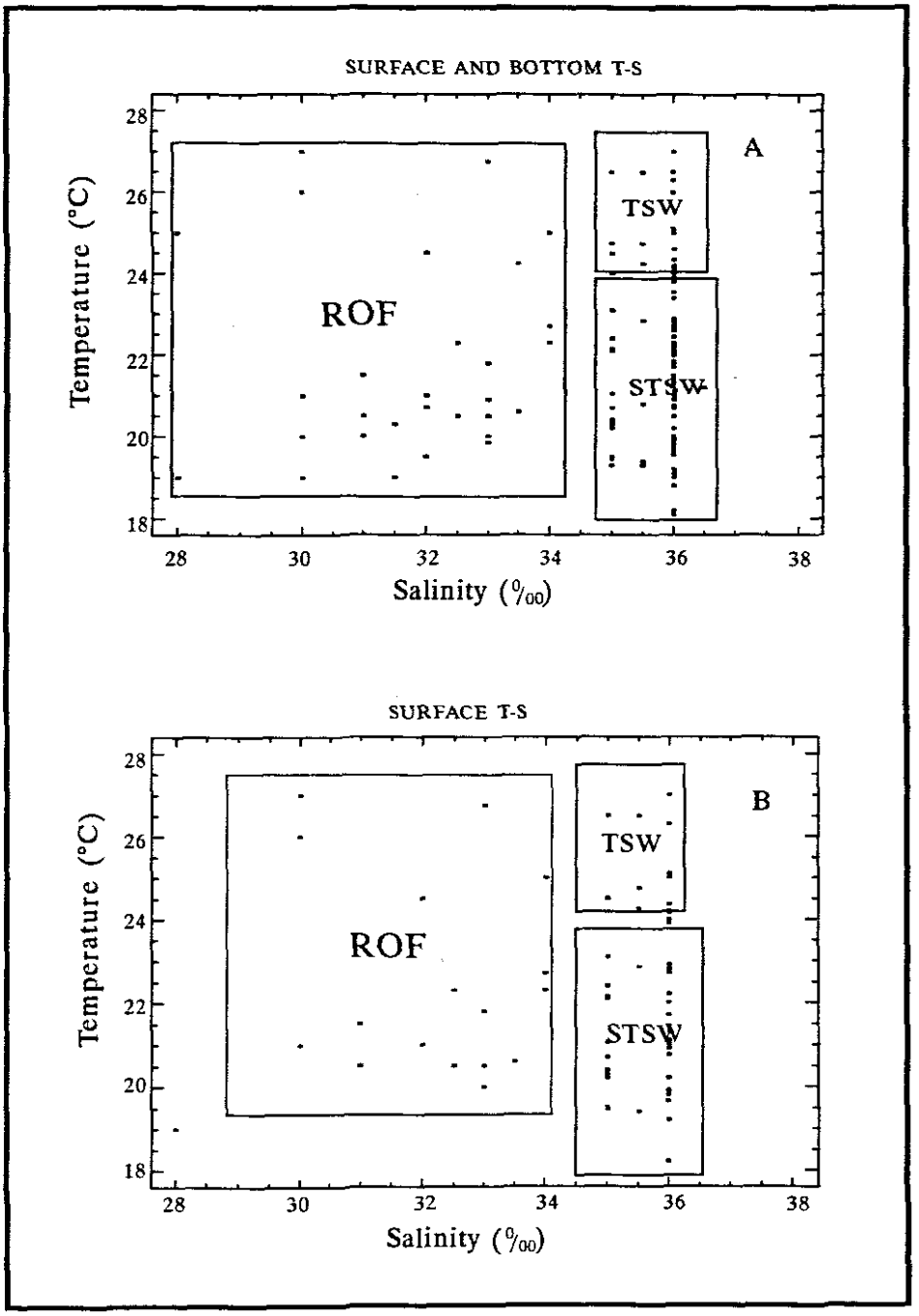


Figure 9.3. Temperature/salinity distribution of surface and bottom (A) and surface (B) values, measured in the nearshore coastal zone from July 1990 to June 1991. (ROF, river outflow; TSW, tropical surface water; STSW, subtropical surface water).

9.2.2. Assemblage Composition and Relationships to Environmental Variables

A total of 6 069 larvae, representing 98 families and 246 taxa, was collected between July 1990 to June 1991 (Table 9.1 and Appendix V). The two most abundant families were Myctophidae and Tripterygiidae comprising 21.3% and 15.7% of the total catch, respectively (Figure 9.4). Other abundant families were Clupeidae (7.1%), Bregmacerotidae (6.4%), Gobiidae (6.7%), Blenniidae (3.9%) and Scombridae (3.5%). Families contributing 1 - 3% of the total catch were Bothidae (2.9%), Leiognathidae (2.9%), Gobiesocidae (2.8%), Carangidae (2.0%), Callionymidae (1.6%) and Sparidae (1.1%).

Four species contributed more than 5% of the total catch: Tripterygiid 1 (9.2%), *Benthosema fibulatum* (8.7%), *Etrumeus teres* (5.6%) and *Benthosema pterotum* (5.5%). Other relatively abundant species were, in order of abundance, Gobiid 4 (4.5%), Tripterygiid 1 (4.2%), *Bregmaceros atlanticus* (3.8%), *S.holodon* (3.2%), *Rastrelliger kanagurta* (2.7%), *Bregamceros nectabanus* (2.7%), *Engyprosopon grandisquama* (2.6%) and Blenniid 6 (2.6%) (Table 9.1).

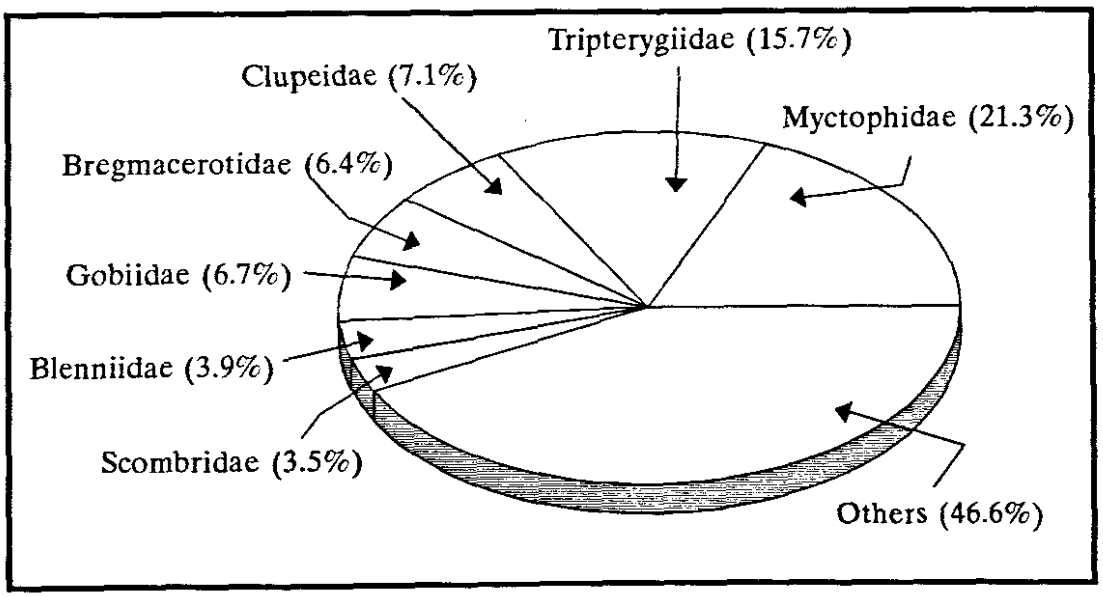


Figure 9.4. Percentage contribution of dominant families for all taxa collected in the study.

Table 9.2. Total catch, body length and developmental stage for all larvae collected in the nearshore coastal zone off the St Lucia Estuary mouth.

Family	Species	Overall Rank	Total catch			Body length (mm)			Developmental stage
			no.	density (mean no.100m^{-3})	% of total	Mean	Min	Max	
ESTUARINE DEPENDENT									
Estuarine residents									
Clupeidae	*Gilchristella aestuaria*		2	0.01	<0.1	19.3	13.0	25.5	Po,Ju
Gobiidae	*Psammogobius knysnaensis*		3	0.01	<0.1	5.0	4.0	6.4	Po
	Taenioides jacksoni		2	0.01	<0.1	9.8	9.5	10.0	Po
Marine spawners dependent on estuaries									
Teraponidae	*Terapon jarbua*		11	0.06	0.2	4.7	3.5	10.0	Pr,Fl,Po
Haemulidae	*Pomadasys commersonnii*		2	0.01	<0.1	9.8	7.5	12.0	Po
Sparidae	*Rhabdosargus sarba*		17	0.09	0.3	6.2	4.0	10.0	Pr,Fl,Po
Monodactylidae	*Monodactylus argenteus*		3	0.02	0.1	5.0	4.0	6.0	Po
PARTIALLY ESTUARINE DEPENDENT									
Catadromous									
Megalopidae	*Megalops cyprinoides*		2	0.01	<0.1	26.3	25.5	27.0	Le
Estuarine and marine spawners									
Syngnathidae	*Syngnathus acus*		8	0.04	0.2	15.5	9.0	30.0	Po,Ju
	Hippichthys heptagonus		11	0.05	0.2	11.2	8.5	20.0	Po
Ambassidae	*Ambassis* sp.		32	0.16	0.6	3.9	3.0	5.0	Pr,Po
Gobiidae	*Croilia mossambica*		62	0.25	0.9	8.9	5.2	13.0	Po
	Taenioides esquivel		1	<0.01	<0.1	10.0	10.0	10.0	Po
Marine spawners with juveniles abundant in estuaries									
Mugilidae	Mugilid spp.		3	0.02	0.1	4.9	2.6	8.5	Pr,Po
Soleidae	*Solea bleekeri*		26	0.14	0.5	2.6	1.5	14.0	Pr,Po

cont.

Marine spawners with juveniles at sea and in estuaries									
Engraulidae	*Stolephorus holodon*	8	200	0.85	3.2	14.2	3.2	45.0	Pr,Fl,Po,Ju
Chanidae	*Chanos chanos*		14	0.07	0.2	12.0	10.0	14.0	Po
Hemiramphidae	*Hyporhamphus impravisus*		5	0.03	0.1	10.0	5.7	14.0	Po
Platycephalidae	*Platycephalus indicus*		8	0.05	0.2	4.5	3.0	6.0	Pr,Fl
Teraponidae	*Pelates quadrilineatus*		1	<0.01	<0.1	12.0	12.0	12.0	Po
Haemulidae	*Pomadasys kaakan*		13	0.05	0.2	6.0	5.0	8.0	Fl,Po
Lutjanidae	*Lutjanus argentimaculatus*		8	0.04	0.1	6.1	3.0	12.0	Pr,Po
Gerreidae	*Gerresp* sp. 1		48	0.25	0.9	4.1	3.0	9.5	Pr,Fl,Po
Sillaginidae	*Sillago sihama*		30	0.13	0.5	7.1	3.5	12.5	Pr,Fl,Po
Leiognathidae	*Leiognathus equula*	17	69	0.35	1.3	3.9	2.2	8.0	Pr,Po
Sphyraenidae	*Sphyraena jello*		3	0.01	0.0	7.3	7.0	8.0	Po
ESTUARINE INDEPENDENT[A]									
Reef and shore taxa									
Clupeidae	*Herklotsichthys quadrimaculatus*	19	62	0.30	1.1	14.8	4.0	20.0	Pr,Fl,Po
	Etrumeus teres	3	305	1.52	5.6	8.3	4.0	25.0	Pr,Fl,Po
Synodontidae	*Trachinocephalus myops*		27	0.12	0.4	8.4	3.0	39.0	Pr,Fl,Po,Ju
Bregmacerotidae	*Bregmaceros atalnticus*	7	213	1.01	3.8	4.3	2.0	14.0	Pr,Fl,Po
	Bregmaceros nectabanus	9	163	0.74	2.7	6.3	2.5	13.0	Pr,Fl,Po
Gobiesocidae	*Lepadichthys* sp.1		38	0.15	0.5	5.2	2.5	44.0	Pr,Fl,Po
	Lepadichthys sp.2	14	147	0.48	1.8	4.9	2.5	12.0	Pr,Fl,Po
	Gobiesocid 2		28	0.13	0.5	4.5	2.5	7.0	Pr,Fl,Po
Sparidae	Sparid 3		30	0.15	0.6	4.1	2.5	11.0	Pr,Fl,Po
Nemipteridae	*Nemipterus* sp.		47	0.24	0.9	4.6	3.2	6.0	Pr,Fl,Po
Mullidae	Mullid 1		36	0.21	0.8	5.4	3.5	8.5	Pr,Fl,Po
Leiognathidae	*Secutor insidiator*	15	115	0.44	1.6	4.5	2.5	7.0	Pr,Fl,Po
Carangidae	*Scomberoides* sp.		14	0.10	0.4	5.7	3.0	14.0	Pr,Fl,Po
	Carangid 1		37	0.20	0.8	4.5	2.0	13.0	Pr,Fl,Po
Pempheridae	*Pempheris* sp.2		23	0.12	0.4	3.0	2.5	4.2	Pr
Trichonotidae	*Trichonotus marleyi*		37	0.15	0.6	12.1	7.0	17.0	Fl,PO
Blenniidae	*Istiblennius* sp.		50	0.28	1.0	5.7	2.5	16.0	Pr,Fl,Po
	Blenniid 6	12	142	0.70	2.6	3.7	2.0	9.0	Pr,Fl,Po
Tripterygiidae	Tripterygiid 1	1	490	2.49	9.2	4.9	2.5	44.0	Pr,Fl,Po
	Tripterygiid 2	6	218	1.14	4.2	5.3	3.0	10.0	Pr,Fl,Po
	Tripterygiid 3	13	111	0.62	2.3	4.8	4.0	11.0	Pr,Fl,Po
Callionymidae	*Draculo celatus*	16	105	0.40	1.5	3.4	2.0	6.5	Pr,Fl,Po
Gobiidae	Gobiid 4	5	311	1.23	4.5	3.7	2.0	8.0	Pr,Fl,Po
	Gobiid 12		31	0.13	0.5	5.4	3.2	7.8	Pr,Po
	Gobiid 16		18	0.10	0.4	4.2	3.0	6.0	Pr,Fl,Po

cont.

Table 9.1 cont.

Scombridae	*Rastrelliger kanagurta*	10	260	0.72	2.7	8.0	2.0	22.5	Pr,Fl,Po
	Scombrid 2		25	0.13	0.5	3.1	3.0	3.5	Pr
Bothidae	*Engyrosopon grandisquama*	11	175	0.71	2.6	8.6	2.4	27.0	Pr,Fl,Po
Cynoglossidae	Cynnoglossid 1		14	0.12	0.5	9.1	6.0	14.0	Pr,Fl,Po
Oceanic taxa									
Photichthyidae	*Vinciguerria attenuata*	18	67	0.31	1.1	9.0	4.6	16.0	Pr,Fl,Po
Gonostomatidae	*Cyclothone pseudopallida*		55	0.20	0.7	7.8	4.0	14.0	Pr,Fl,Po
Myctophidae	*Benthosema pterotum*	4	353	1.47	5.5	5.1	3.0	8.0	Pr
	Benthosema fibulatum	2	590	2.36	8.7	4.4	2.0	7.0	Pr,Fl
	Benthosema suborbitale		24	0.11	0.4	4.4	2.8	6.5	Pr,Fl,Po
	Hygophum hygomii		56	0.21	0.8	5.2	3.0	9.0	Pr,Fl,Po
	Hygophum proximum		36	0.16	0.6	4.6	3.3	6.4	Po
	Diaphus sp.2		44	0.22	0.8	5.5	3.8	8.0	Po
	Lampanyctus lepidolychnus		38	0.15	0.6	4.4	3.0	8.0	Fl,Po
	Scopelopsis multipunctatus		53	0.22	0.8	4.3	3.0	6.6	Pr,Po
	Diogenichthys pangurgus	20	70	0.30	1.1	4.4	2.5	18.0	Pr,Po
	Notoscopelus resplendens		28	0.10	0.4	4.8	3.7	7.4	Fl

Total number of larvae = 6064
Number of families = 98
Number of taxa = 246
Unidentified taxa = 10

[A]taxa contributing to < 0.3% of total catch are listed in Appendix V

Stepwise regression analysis showed that only a small percentage (≤ 10%) of the variation in larval densities was accounted for by the environmental variables measured (Table 9.2). Note, however, that temperature and salinity were significant variables for estuarine-independent taxa ($P < 0.001$ and $P < 0.01$, respectively), and that turbidity and salinity were significant for partially estuarine-dependent taxa ($P < 0.001$ and $P < 0.05$, respectively). Overall, the dominant factor affecting larval densities was temperature, particularly for Tripterygiid 1 where temperature composed 9.0% of the variance model.

Table 9.2. Stepwise regression statistics of larval fish densities versus environmental variables (sa, salinity; te, temperature; tu, turbidity) for each estuarine-association group and the most abundant species in each group, in Durban Harbour. (adj; adjusted R^2; coefficient of determination; R, correlation coefficient; F, F statistic)

Estuarine-association group	adjR^2	R	F	significant variables
All taxa	0.06	0.25	13.17***	-te***; sa**
Estuarine-dependent	–	–	–	–
Partially estuarine-dependent	0.03	0.17	7.08**	tu**; sa*
Stolephorus holodon	0.05	0.22	11.85***	tu***; sa*
Estuarine-independent[A]	0.10	0.32	21.80***	-te***; sa**
Tripterygiid 1	0.09	0.30	41.47**	-te***
Gobiid 4	0.04	0.20	9.88***	-te***; sa*
Etrumeus teres	0.05	0.22	10.82***	-te***; sa*
Bregmaceros atlanticus	0.01	0.32	4.14*	-sa*
Benthosema fibulatum	0.04	0.20	9.76***	-te***; sa*

P<0.05; **P<0.01;***P<0.001
[A]not enough data for analysis

9.2.3. Estuarine-Association

Larvae of marine spawners independent of estuaries were the most abundant and dominated the catch both in terms of density (90.0%) and in terms of number of taxa (89.3%) (Figure 9.5). Larvae of estuarine-associated species were present but only contributed to 10.0% in terms of density and 10.8% in terms of number of taxa (Figure 9.5 and Table 9.1). A few specimens of estuarine resident species and marine spawners dependent on estuaries were collected but contributed to < 1% of the total density. Partially dependent taxa were moderately abundant (9.3%) with 18 taxa being recorded.

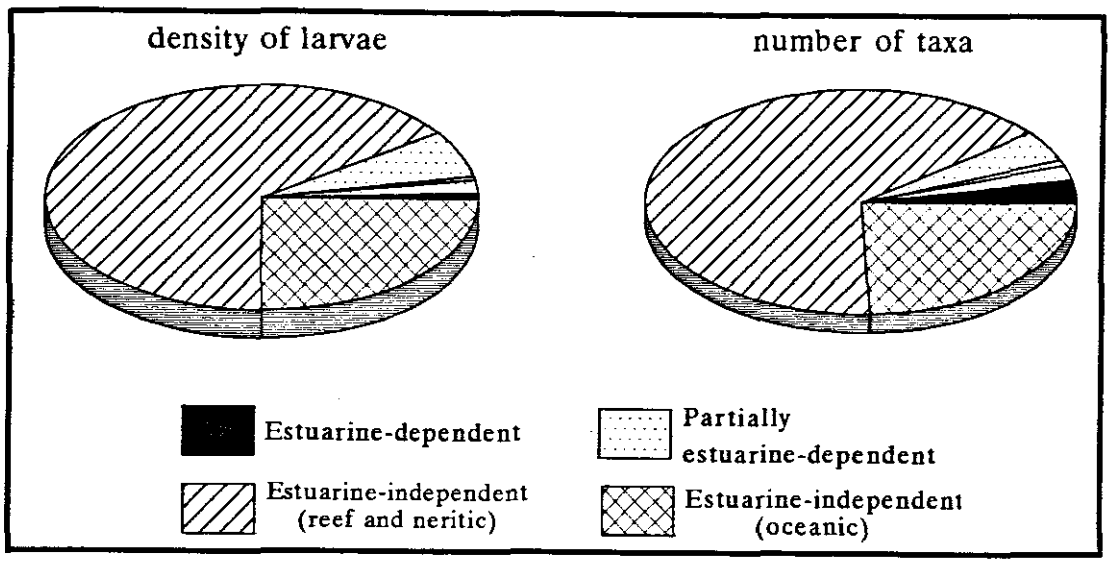


Figure 9.5. Percentage contribution of the estuarine-association categories, in terms of density of larvae and number of taxa, for all taxa sampled in the study.

9.2.4. Temporal and Spatial Trends in Larval Fish Density

Larval densities of all taxa were most abundant in November and December 1990 where the mean density was 49 larvae per $100m^3$ in the bottom samples (Figure 9.6A). The lowest mean density of larvae occurred in the top samples in January 1991 (2.7 larvae per $100m^3$). Very low densities of estuarine-dependent taxa were present but were most abundant in December 1990 (1 larva per $100m^3$) and April 1991 (1.5 larvae per $100m^3$) (Figure 9.6B). Larval densities of partially estuarine-dependent taxa were relatively low but also had a peak in April 1991 (3.2 larvae per $100m^3$) which was due to an abundance of larval *Leiognathus equula, Croilia mossambica* and *Gerres* sp.1 (Figures 9.6C and 9.7). Larvae of certain partially dependent taxa were also abundant from January to March 1991 (Figure 9.7). The dominance of estuarine-independent taxa is clear and as a consequence the seasonal trend is very similar to that of all taxa combined (Figure 9.6A and B).

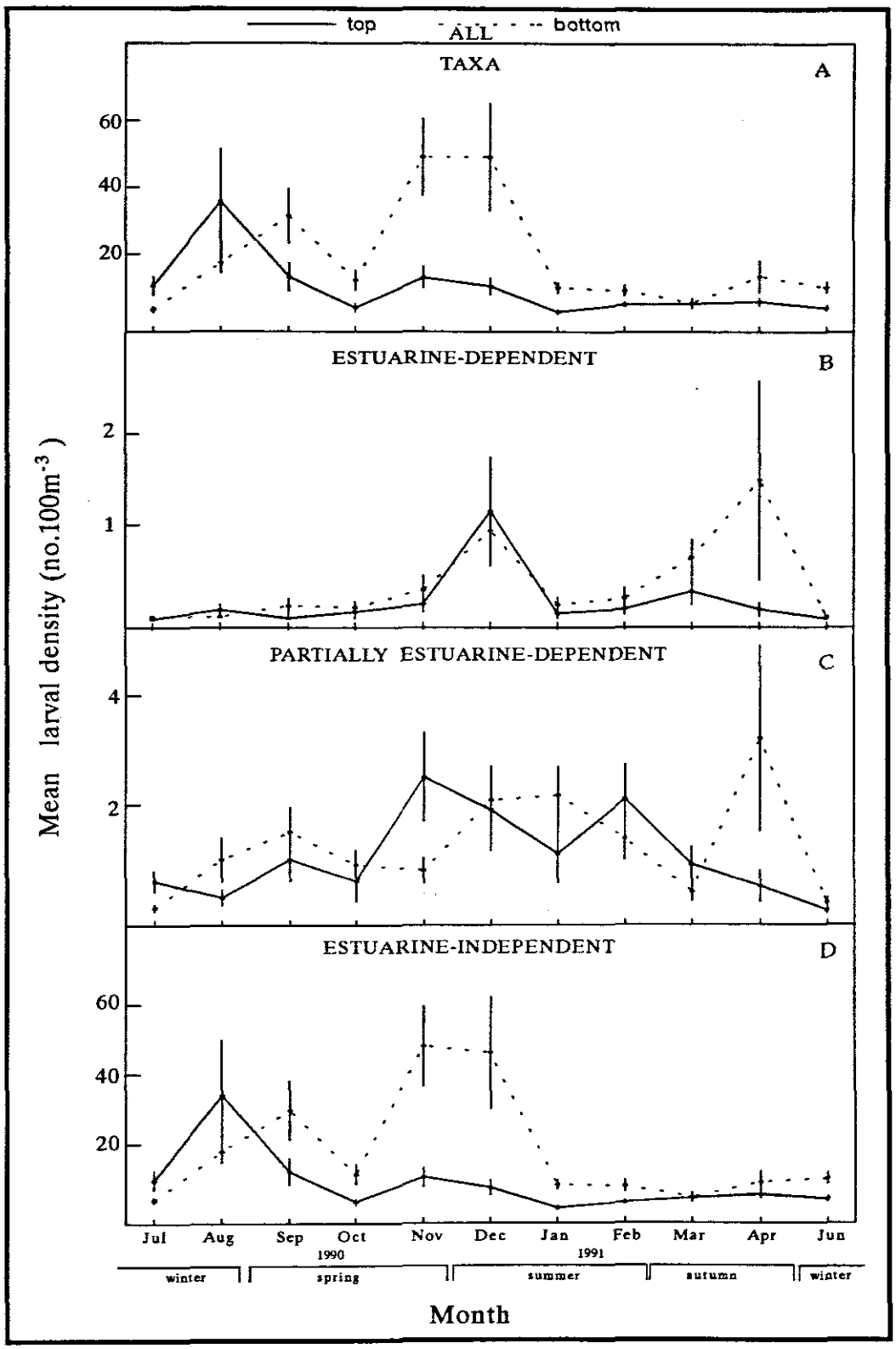


Figure 9.6. Mean monthly variations in larval densities (± 1SE) in top and bottom samples for all taxa together (A), estuarine-dependent taxa (B), partially estuarine-dependent taxa (C) and estuarine-independent taxa (D).

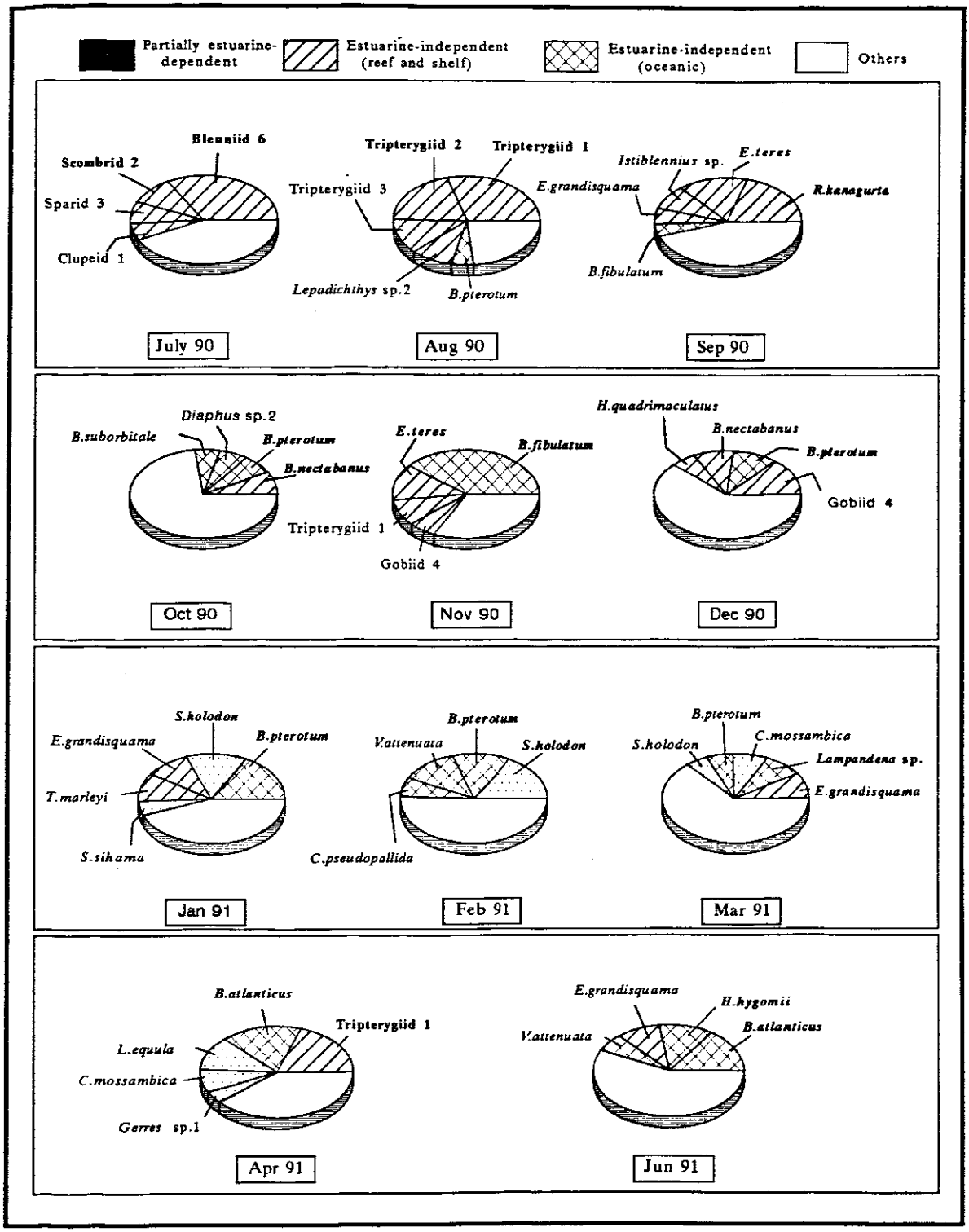


Figure 9.7. Percentage contribution of the most abundant species in the total catch sampled each month.

Different taxa dominated each month with reef- and shelf-associated species accounting for the peak in August and September 1990, oceanic species in November 1990 and a mixture of the two groups in December (Figures 9.6D and 9.7).

Three-way ANOVAs showed that larval densities were significantly much greater in bottom samples than in top samples for all taxa together but were group and species specific (Table 9.3). The mean square for the estuarine-independent group was particularly high with only one of the dominant species, Tripterygiid 1, having significantly higher densities in top samples ($P < 0.001$). Significant differences in larval densities between stations were found for some groups and individual species (Table 9.3). For estuarine-independent taxa densities were only significantly higher at station 4 compared with station 7 (Figure 9.8) although a trend of increasing densities with distance offshore was evident. Densities were also higher at station 1 (closest to estuary mouth) than at station 6 (north of estuary mouth) and station 7 (south of estuary mouth) but this was not significant. The few larvae of estuarine-associated species that were present occurred randomly at all 7 stations (Figure 9.8B and C). Although month was a significant factor for all groups, except estuarine-dependent species, the mean squares were relatively small (Table 9.3). The depth x station interaction was significant for the estuarine-independent group, particularly for *B.atlanticus* ($P < 0.001$). The depth x month interaction was significant mainly for estuarine-independent taxa, whilst the station x month interaction was not significant overall.

Table 9.3. Mean squares and significancelevels for three way ANOVAs of densities of the most abundant species in each estuarine-association group, in the nearshore coastal zone off the mouth of the St Lucia Estuary. (DF, degrees of freedom)

Estuarine-association group	Main effects			2-way interaction		
	Depth (T,B)[A] (DF=1)	Station (1 to 7)[B] (DF=6)	Month (1 to 11)[C] (DF=10)	Depth x Station (DF=6)	Depth x Month (DF=10)	Station x Month (DF=20)
All taxa	6.66***(B>T)	0.53***	1.7***	2.51***	0.68***	0.26
Estuarine-dependent	0.12**(T>B)	0.01	0.01	0.02	0.01	0.02*
Partially estuarine-dependent	0.63*(B>T)	0.05	0.51***	0.19	0.15	0.13*
Stolephorus holodon	<0.01	0.04	0.20***	0.08	0.07*	0.06*
Estuarine-independent	8.18***(B>T)	0.60*	1.91***	2.20***	0.80***	0.27
Tripterygiid 1	1.11***(T>B)	0.26**	0.80***	0.19*	0.29***	0.13**
Gobiid 4	1.11***(B>T)	0.02	0.27***	0.03	0.12***	0.09
Etrumeus teres	0.71***(B>T)	0.17*	0.34***	0.12*	0.16***	0.07
Bregmaceros atlanticus	1.10***(B>T)	0.33***	0.12**	0.31***	0.06	0.05
Benthosema fibulatum	1.15***(B>T)	0.13	0.75***	0.08	0.74***	0.12

*p < 0.05; **p < 0.01; ***p < 0.001

[A]depths where densities are significantly higher are indicated in parentheses. T, top; B, bottom

[B]stations where densities are significantly higher are indicated in Fig. 9.8 (Groups only)

[C]months where densities differ significantly are indicated in Fig .9.6 (Groups only)

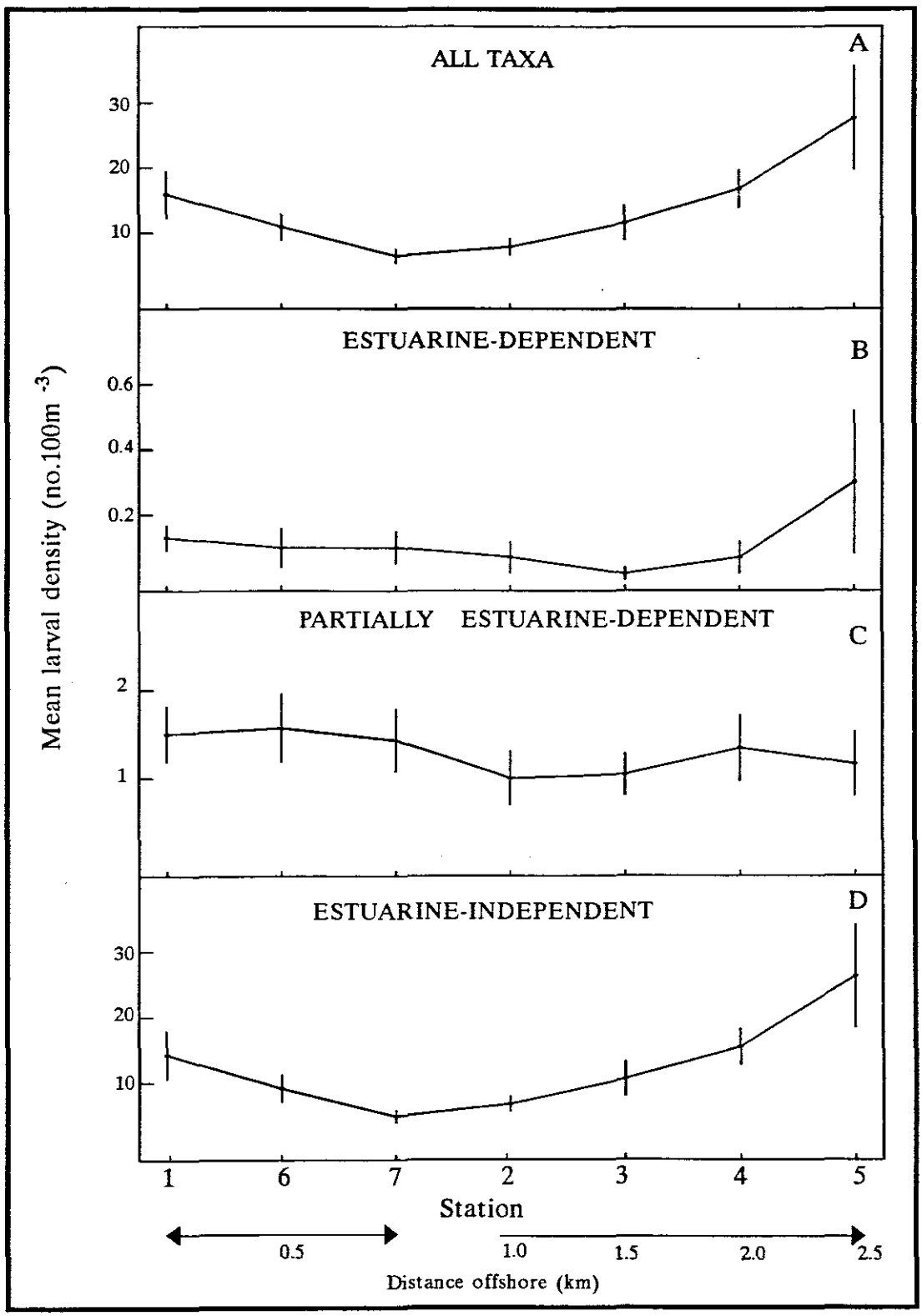


Figure 9.8. Mean variations in larval densities (± 1SE) at each station along the transect in the nearshore coastal zone off the St Lucia Estuary mouth for the study period.

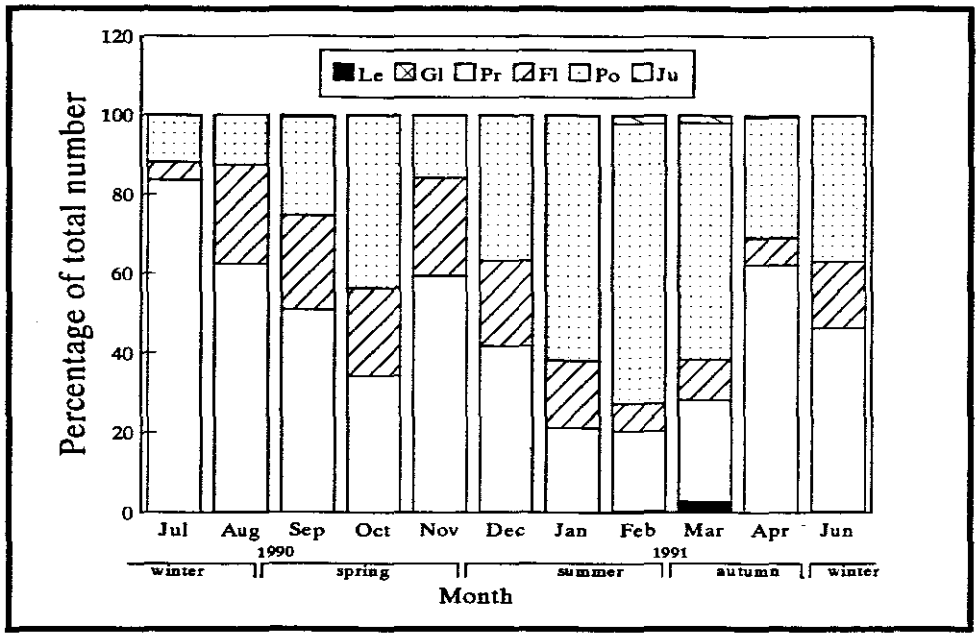


Figure 9.10. Monthly percentage composition of developmental stages of all larvae sampled in the study. Gl, glass eel; Le, leptocephali; Ys, yolk sac; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile.

The larvae of the abundant species in each estuarine-association group had different ontogenetic distribution patterns with respect to station/distance offshore (Figure 9.11). The larvae of *C.mossambica*, a goby which breeds in estuaries and at sea, were only present as postflexion larvae and were most abundant at station 1 and 6 in bottom waters. A few specimens also occurred at the stations further offshore (station 2, 3 and 4) but only in bottom samples. The engraulid *S.holodon*, a species abundant at sea and in estuaries, was present mainly as postflexion larvae but some flexion and juvenile specimens were also present. Larvae of *S.holodon* were predominantly in bottom samples at all stations with larvae being most abundant at stations 1 and 4 - i.e. no trend with distance offshore. The reef species, Tripterygiid 1 and Gobiid 4, were present as young and old larvae and were most abundant at the stations closest to shore (stations 1 and 6). The clupeid *E.teres* and the codlet *B.atlanticus* are pelagic species and showed a definite trend in increasing numbers with distance offshore and were predominantly in bottom waters (Figure 9.11). Developmental stages of these two species were mainly young larvae. The oceanic lanternfish *B.fibulatum* was only present in bottom samples with preflexion and flexion stages being most abundant further offshore.

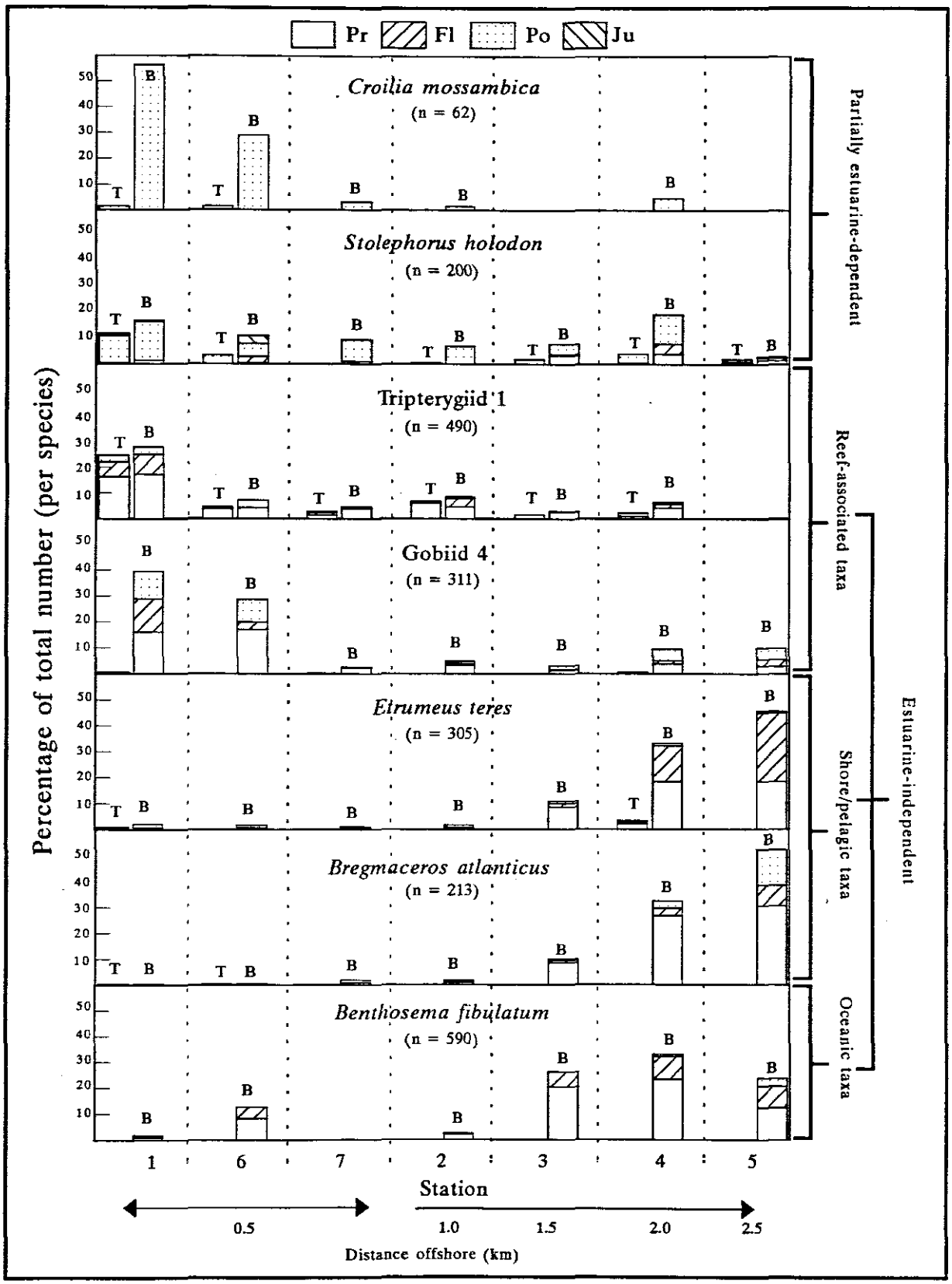


Figure 9.11. Changes in proportions of different developmental stages of the dominant taxa at each station along the transect. (T, top; B, bottom; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile; n, total number of larvae).

9.3. Discussion

9.3.1 Composition of the Larval Fish Assemblage

The composition of a larval fish assemblage in nearshore coastal zones is related to the local current regimes and water masses occurring in the region. The occurrence of oceanic/slope-spawning species such as *Vinciguerria* sp., *Cyclothone* sp. and myctophid species are good indicators of slope water (John 1984; Belyanina 1986; Cowen *et al.* 1993; Chiu and Hsyu 1994). On the south-east coast of South Africa, the presence of larvae of mesopelagic myctophids over the continental shelf has been closely linked to shoreward intrusions of Agulhas Current surface water (Olivar and Beckley 1994b). In the present study, larval myctophids were particularly abundant with *B.fibulatum and B.pterotum* ranking second and fourth overall and 23 of the 30 myctophid species (including the latter two species) recorded off St Lucia were also recorded by Olivar and Beckley (1994b) from the Agulhas Current ichthyoplankton survey. This indicates that the Agulhas Current has a major influence on the composition of the larval fish assemblage in the nearshore coastal zone in the St Lucia region. The influence of the East Australian Current on ichthyoplankton communities was also noted by Miskiewicz (1987): the presence of larvae of mesopelagic species in Lake Macquarie (New South Wales) was attributed to periodic intrusions of slope water onto the shelf region due to variations in the flow of the East Australian Current.

Although Agulhas Current surface water had an influence of the composition of fish larvae in the shelf waters off St Lucia, larvae of other "typical" shelf species were also relatively abundant. For example, the scombrid *R.kanagurta* (Indian mackerel) was relatively abundant (ranked 10th overall) and is a neritic species widespread in the Indo-Pacific (Smith and Heemstra 1986). Larvae of *Rastrelliger* were also recorded in abundance in a coastal bay of the Andaman Sea (southern Thailand) (Janekarn and Kiørboe 1991). Forty-six of the 48 taxa recorded in the coastal bay of the Andaman Sea, were also recorded in the coastal zone off St Lucia (Table 9.1). Also of note, was the presence of many larvae of two codlet species, *Bregmaceros nectabanus* and *B. atlanticus*, which are small gadiform fishes found in neritic and oceanic waters in both tropical and subtropical waters (Houde 1984).

Chiu and Hsyu (1994) found that the species composition of the larval fish assemblage in the coastal zone of the East China Sea indicates a complicated environment that included three biotopes: neritic, slope and oceanic. Like the KwaZulu-Natal coast, the shelf region of the East China Sea is also influenced by a dominant western boundary current, the Kuroshio Current. The larval fish assemblage in the coastal waters off St Lucia was very similar to that recorded by Chiu and Hysu (1994), in terms of total numbers of larvae, number of taxa and number of families (5803 larvae, 91 families and 254 taxa - their study; 6 069 larvae, 98 families and 246 taxa - present study). Thus, the marine environment on the continental shelf off St Lucia is also characterised by the three biotopes, neritic, slope and oceanic, but has an additional estuarine component.

Larval fish assemblages in coastal shelf waters are influenced by physical processes such as oceanographic features (Olivar 1990; Kingsford *et al.* 1991; Beckley 1993) and proximity to reefs (Kingsford and Choat 1989; Tilney and Buxton 1994). Larval fish studies in the nearshore waters in the Eastern Cape (Algoa Bay and Tsitsikamma - see Figure 2.1, Chapter 2) reported different types of assemblages to the assemblage off St Lucia with dominant families being more representative of inshore reef fish communities (Beckley 1986; Tilney and Buxton 1994). Dominant families were Gonorhynchidae, Sparidae, Gerreidae, Cheilodactylidae, Gobiidae, Blenniidae, Carangidae and Gobiesocidae. Since the continental shelf in the Eastern Cape widens considerably south of the Great Fish River (see Figure 2.1, Chapter 2), the influence of the Agulhas Current is not felt as strongly, resulting in a different type of larval fish assemblage to that found off St Lucia. The proximity of reefs, particularly in the Tsitsikama National Park, must be the dominant physical feature influencing the composition of the larval fish community in this region. Tzeng and Wang (1993) found that most of the fish larvae in their study (65% of total catch), in the coastal waters off the Tanshui River Estuary (Taiwan), were estuarine-associated species e.g. *Liza macrolepis*, *Ambassis gymnocephalus* and *Terapon jarbua.* Their study area was also located on a shallow and wide continental shelf with little influence of major current systems.

9.3.2 Larval Abundance in Relation to Environmental Factors

The extent of onshore migration of estuarine fishes is dependent on their tolerance to extremes of environmental variables (Whitfield *et al.* 1981; Shaw *et al.* 1985; Boehlert and Mundy 1988). Whitfield (1994c) suggested that olfactory cues associated with riverine inputs and hence estuarine outflow stimulate immigration of euryhaline fishes into estuaries and not salinity per se, although salinity gradient was the most important factor in his study. In the coastal waters of the Tanshui River Estuary, the abundance of larvae of dominant estuarine-associated species (*Liza macrolepis* and *Ambassis gymnocephalus*) were negatively correlated with salinity (Tzeng and Wang 1993). This also suggested that low salinity may act as a cue to guide fish larvae and juveniles to inshore nursery grounds. Salinity was negatively correlated to larval densities of estuarine-associated taxa within the St Lucia Estuary (Table 6.1, Chapter 6) but not in the nearshore coastal habitat where salinity was positively correlated to larval densities (Table 9.2). However, salinity together with either temperature or turbidity did not account for much of the variability in larval densities of estuarine-associated taxa in the nearshore coastal zone (< 6% of the regression model). In the nearshore waters off the Tanshui River Estuary (Taiwan) larval densities of the most abundant estuarine-associated species had a negative correlation with salinity which was due to the greater estuarine influence on a shallow and wide continental shelf (Tzeng and Wang 1993).

Blaber and Blaber (1980) suggested that turbidity gradients in the marine environment may aid juvenile fishes to locate estuarine nursery areas. In the present study, a turbidity gradient exists from the nearshore marine environment → surf zone habitat → estuarine habitat (see Figure10.5, Chapter 10). Note also, that on the gradient from nearshore to estuarine habitat, turbidity accounts for a greater percentage of the variability in larval densities i.e. in the coastal waters off St Lucia, turbidity and salinity were significant factors for larvae of partially estuarine-dependent taxa, although only accounting for 3% of density variations; in the St Lucia Estuary, turbidity and temperature accounted for 29% of the variation in larval densities (see significant variables in Table 10.1, Chapter 10). This suggests that larvae of fish species associated with estuaries are also responding to changes in water turbidities. Other factors must also be important, since, several physical factors near estuaries serve as "point source"

stimuli that could elicit short-term behavioural responses by larvae (Boehlert and Mundy 1988).

Temperature is an important environmental variable influencing ichthyoplankton assemblages in coastal waters and is related to seasonality patterns of larval fish abundance (Belyanina 1986; Kingsford 1988; Tzeng and Wang 1993) and was a significant variable in the coastal waters off St Lucia Estuary. This was particularly so for Tripterygiid 1 where larval densities were negatively correlated with temperature $P < 0.001$). This was related to the seasonal changes in abundance of larval tripterygiids which were particularly abundant in the winter month of August 1991 (see Figure 9.7) when temperatures were lower (< 20°C). Tricklebank *et al.* (1992) similarly recorded a peak abundance in tripterygiids larvae in the coastal waters off north-eastern New Zealand during winter months. In addition, the larvae of Tripterygiid 1 were more abundant in the inshore cooler waters than the offshore warm Agulhas Current waters (Figure 9.11).

Since the environmental variables measured during the present study only accounted for a small percentage of variations in larval density, other environmental factors not measured in this study (e.g. hydrographic features such as longshore currents, upwelling and eddies) must also play an important role in recruitment to inshore nursery grounds.

9.3.3. Temporal and Spatial Trends in Larval Fish Abundance

In tropical and subtropical coastal waters significant variations in densities of larval fishes occur both temporally and spatially (Belyanina 1986; Soewito and Schalk 1990; Gray 1993; Tzeng and Wang 1993; Chiu and Hysu 1994). Seasonal and spatial patterns in abundance of fish larvae in the nearshore coastal waters of the present study were also evident. These patterns of larval abundance were specific to estuarine-association group and to individual species (Figure 9.11).

Overall seasonality patterns in coastal shelf waters are often reflected in the abundance of dominant taxa (Grabe *et al.* 1992; Tricklebank *et. al.*, 1992). In the present study, this was clearly the case and was related to dominant taxa in a particular estuarine-association group. These temporal abundance patterns arise due to the

interactive effects of abiotic and biotic factors. Abiotic factors include seasonal variations in environmental variables, such as temperature, and local climatic conditions which affect the water current patterns. Local upwelling events on the Tsitsikamma coast, in the Eastern Cape, impacted negatively on larval fish abundance (Tilney and Buxton 1994). Biotic factors are also related to food availability: Haldorson *et al.* (1992) have shown that seasonality of abundant larval fish taxa in Auke Bay (Alaska) is related to the abundance of zooplankton and Monteleone (1992) found that the seasonality of abundance of larval fish in Great South Bay (New York) was strongly correlated with densities of copepod nauplii. Variability in zooplankton biomass in KwaZulu-Natal shelf waters has been shown to occur with Agulhas Current water having a lower plankton biomass compared to inshore areas (Carter and Schleyer 1978). In the shelf waters off Richards Bay plankton biomass varies on time scales of days and spatial scales of tens of kilometres (Carter 1973).

The spatial patterns in larval composition and abundance in both horizontal (onshore-offshore and longshore directions) and vertical (with depth) in coastal shelf waters vary considerably and seem to depend on the physical topography and local current regimes. In nearshore coastal waters, horizontal trends in larval fishes abundances and composition are seen more in the onshore-offshore direction (Richardson *et al.* 1980; Young *et al.* 1986; Sabates 1990; Tricklebank *et al.* 1992; Gray 1993) than in the longshore direction. Both onshore-offshore and alongshore patterns in larval fish distribution were apparent in the nearshore waters off St Lucia, with the greatest density occurring at both inshore and offshore stations which were group and species-specific. The abundance of larvae at the station 1 closest to shore indicates an accumulation of larvae at this location of both reef and estuarine-associated species (Figure 9.11). A study of the larval fish in the surf zone (Chapter 8) similarly recorded higher densities of larval fish at the stations nearest the mouth, particularly when the estuary mouth was closed. Some studies have reported higher densities of larvae and number of taxa more inshore (Barnett *et al.* 1984) and others more offshore (Sebates 1990; Tricklebank *et al.* 1992; Gray 1993) and that it is species-specific (Tricklebank *et al.* 1992; Gray 1993). Distribution of adult fish, their spawning location and the type of eggs they produce (pelagic or demersal) accounts for horizontal patterns in larval abundance in tropical and temperate coastal waters (Leis and Miller 1976; Beckley 1986;

Marlieve 1986; Sebates 1990; Gray 1993; Tilney and Buxton 1994). For example, tripterygiid larvae are particularly abundant inshore (Leis and Goldman 1984; Kingsford and Choat 1989; Tricklebank *et al.* 1992; Leis 1993; and this study). This is related to their spawning mode (demersal eggs) and the fact that they remain near their natal reefs (Leis 1991). Similarly, for estuarine-associated taxa which have demersal eggs (e.g. gobies) were found closest to shore, and those with pelagic eggs had variable distances from shore. Beckley (1986) found a paucity of sparid larvae in her samples but the stations were only behind the breaker line and suggested they are found further offshore.

Some taxa move shorewards with increasing age prior to settlement (Jennings and Pawson 1992) or show no trend (Leis 1982; Kingsford 1988; Kingsford and Choat 1989). Results of the present study indicated that this depends on the degree of estuarine-association of a species and its developmental stage which would determine the swimming ability of the larva. Certain fish species use ontogenetic behavioural changes to enhance shoreward movement of larvae (Tzeng and Wang 1992). Such ontogenetic changes in distribution, both horizontally and vertically, are mechanisms for recruitment and retention in nursery areas - particularly in estuarine nurseries (Weinstein *et al.* 1980; Laprise and Dodson 1989). Older larvae of estuarine-associated species were found close inshore in bottom waters whilst the larvae of pelagic and oceanic types were mainly young larvae and more offshore in deeper waters (Figure 9.11).

9.3.4. Transport of Larvae and Proximity to Spawning Grounds

Transportation of fish larvae from offshore to the nearshore waters and then into estuarine nursery areas is influenced both by physical processes as well as the fishes's activity and behaviour (Weinstein *et al.* 1980; Boehlert and Mundy 1987; Tanaka 1985; Shaw *et al.*1985; Tzeng and Wang 1993). Ontogenetic behavioural change associated with developmental stage will therefore play an important role in determining abundance of fish larvae in nearshore waters. A larger mean size in deeper water suggests ontogenetic behavioural changes in distribution which enhance shoreward movement to estuarine nursery sites. Powles (1981) found that the standard lengths of estuarine-dependent species (mugilid spp. and *Pomatomus saltatrix*) were inversely related to distance from shore whilst for estuarine-independent taxa (*Coryphaena* spp.) no

relationship with length of larvae and distance offshore was found.. Although the three studies in the St Lucia region (within the estuary, surf zone and nearshore shelf waters) were sampled in different years the mean size and abundance of selected species of different categories show a definite pattern (Table 9.4). The estuarine-associated species are far more abundant with a larger mean size and larger size range in the estuary and/or surf zone than in the nearshore marine environment - i.e. younger larvae in nearshore coastal zone. Conversely, the reef, shore (neritic) and oceanic species are more abundant in the nearshore environment (or absent in estuary) with a larger size range. Interestingly, the mugilid spp. were most abundant in the surf zone suggesting that this species spends some time in the surf zone before moving into the estuary.

Table 9.4. Mean size (range) and number of larvae of selected species occurring in St Lucia Estuary, the adjacent surf zone and the nearshore marine environment.

Species	Estuary[A]		Surf[B]		Nearshore	
	size(range) (mm)	number of larvae	size(range) (mm)	number of larvae	size(range) (mm)	number of larvae
Estuarine spawners						
Glossogobius callidus	6.7(3.0-40.0)	32585	–	–	–	–
Ambassis sp.	6.2(4.0-12.0)	303	6.6(4.0-23.0)	332	3.9(3.0-5.0)	32
Marine spawners/ estuarine dependent						
Thryssa vitrirostris	19.9(11.0-42.0)	831	17.7(17.0-18.0)	4	–	–
Mugilid spp.	12.8(5.0-23.5)	10	11.5(6.0-24.0)	77	4.9(2.6-8.5)	3
Leiognathus equula	12.8(5.2-27.0)	203	12.5(11.0-14.0)	4	3.9(2.2-8.0)	69
Rhabdosargus sarba	10.3(8.0-12.0)	27	8.4(3.5-11.5)	8	6.2(4.0-10.0)	17
Marine spawners/ reef, shore and oceanic						
Tripterygiid 1	5.9(3.5-9.5)	86	5.7(3.4-15.2)	281	4.9(2.5-44.0)	490
Bregamaceros atlanticus	10.5	2	–	–	4.3(2.0-14.0)	213
Vinciguerria attenuata	–	–	9.5(9.0-10.0)	4	9.0(4.6-16.0)	67
Benthosema fibulatum	–	–	4.8	1	4.4(2.0-7.0)	590
Rastrelliger kanugurta	–	–	–	–	9.0(2.0-22.5)	260

[A]see Table 6.1, Chapter 6
[B]see Table 8.1, Chapter 8

A main factor causing the difference in length at which three sparid larvae enter Lake Macquarie Estuary is the proximity of spawning ground (Miskiewicz 1986). The proximity of the spawning grounds of say *L.equula* can be calculated as follows: if one assumes that *L.equula* larvae hatch at 1.3 mm (size at hatch for *L.theraps* - Leis and Trnski 1989) and grow at say 0.25 mm per day, a larva of 2.2 mm (min size of *L.equula* recorded in nearshore) would be 3.6 days old. This implies the spawning grounds for this species is in close proximity to the St Lucia Estuary. The minimum size for the majority of estuarine-associated taxa recorded in the nearshore zone was in the range 2.2 - 4.0 mm which makes them approximately between four and 14 days old (assuming the larvae hatch at 2 mm and grow at 0.25 mm per day - Leis and Trnski 1989). This indicates close proximity of spawning grounds for these species. Miskiewicz (1987) found that some estuarine taxa which entered the estuary at < 6 mm were absent at the stations offshore also indicating nearshore spawning. However, Shaw *et al.* (1985) noted that larvae of estuarine-associated species do not necessarily recruit to estuaries nearest to their offshore spawning areas and that the water mass movements near the coast could displace larvae several hundreds of kilometres.

Plankton dynamics and distributions in Natal coastal waters are more influenced by physical than biological forces (Carter and Schleyer 1988). A schematic representation of local current regime in the study area is shown in Figure 2.4 (Chapter 2) and shows that currents on the continental shelf of the KwaZulu-Natal coast are predominantly in a southerly direction with a northerly longshore current prevailing within the surf zone (Harris 1978; Shumann 1987). In addition, there are current reversals and occasional onshore ↔ offshore currents. Evidence from bedload partings on the seabed at Cape Vidal (see Figure 2.1, Chapter 2) indicates that a large closed eddy system (clockwise) moves up and down this stretch of coastline (Flemming and Hay 1988). Harris (1978) also indicated clockwise eddy systems to the north and south of Cape St Lucia.. Oceanographic features associated with the shoreward edge of the Agulhas Current retain linefish larvae for southward dispersal to nursery areas (Beckley 1993) with the short-lived larvae of estuarine-associated fishes being dependent upon the inshore current reversals and eddies for retention on the shelf and subsequent recruitment to nurseries (Heydorn 1978). Nearshore retention of early life-history stages is exhibited by most shorefishes in continental shelf waters (McGowen 1993). In summary, a

variable current regime exists off the coast of KwaZulu-Natal that seems favourable for retention of ichthyoplankton on the shelf region

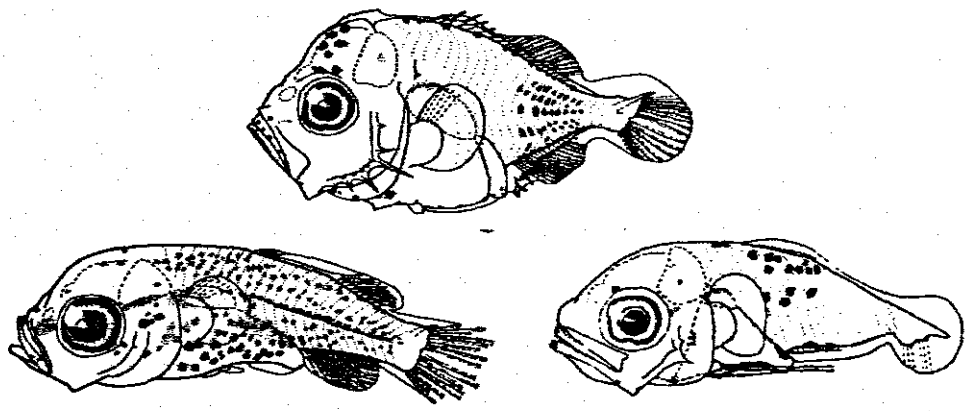
Miskiewicz (1987) found that estuarine-dependent and marine larvae co-occurred in the nearshore zone off Lake Macquarie (3 stations up to 4 km offshore). Larvae of estuarine-associated taxa commonly caught entering Lake Macquarie were rare at the offshore stations indicating nearshore spawning. On the KwaZulu-Natal coast certain estuarine-dependent fish species spawn inshore (e.g. *R.sarba, R.holubi, P.commersonnii* and *Valamugil cunnesius*) and are, therefore, close to their coastal nursery grounds (Wallace 1975b). Beckley (1986) found that representatives of families such as Sparidae and Mugilidae, which numerically dominate juvenile nursery areas in Algoa Bay, were not abundant in the nearshore ichthyoplankton. This suggested that the spawning grounds for these species was not in the immediate vicinity of the study area. Conversely, larvae of marine spawners dependent on estuaries as nursery sites (e.g. *P.commersonnii, A.berda, Argyrosomus* sp. and mullet species) were relatively abundant in Durban Harbour as young and old larvae (Table 4.1, Chapter 4). This indicated nearshore spawning of these species and subsequent recruitment into the harbour system on flood tides. A large number of marine spawned larvae of estuarine-dependent species were collected in the St Lucia Estuary and the adjacent surf zone which were mainly at the postflexion stage (see Table 6.1, Chapter 6, and Table 9.1) also suggesting nearshore spawning

An important question to ask is what is the origin of the larvae in the shelf waters off St Lucia. In other words, where are the spawning sites for these taxa ? Many of the reef fish larvae, for example tripterygiids and gobies, most likely originate from local populations since such taxa are know to settle near their natal reefs (Leis 1991). As far as pelagic species are concerned, such as scombrids (mackerels), clupeiformes (sardine and herring, anchovy) and carangids (scad), many of the larvae originate locally or from spawning populations further north which are carried southwards in the Agulhas Current. Intensive surveys on small pelagic fish stocks have been undertaken on the northern Mozambique coast (Gislason and Sousa 1985). These studies have shown that large spawning populations of species such as *T.vitrirostris, P.ditchella, Decapterus* sp., *Stolephorus* sp., *Trachurus trachurus, R.kanagurta* and *L.equula* exist on the Sofala Bank (approximately 1 100 km north of study area - see insert in Figure 2.1, Chapter 2).

It is possible that larvae from these populations can reach the KwaZulu-Natal coast since it would take a fish larva 13 days to travel 1 100 km if transported in the Agulhas Current at an average speed of $1ms^{-1}$. For example, the scombrid *R.kanagurta* was collected in the size range 2.2 - 22.5 mm (mean 8mm) and if a scombrid larva hatches at say 2.8 mm (scombrids typically hatch between 2.5 and 3.0 mm - Leis and Trnski 1989) and grows at 0.25 mm per day to grow 5.2 mm (8 - 2.8) it would be 21 days old when it reaches the shelf waters off St Lucia. A similar calculation was done for Schindler's fish larvae (*Schindleria praematura* and *S.pietschmanni*) which were collected in samples taken adjacent to the small reef in the Kosi Estuary (see Addendum). Larvae of these species may be originating from a northern spawning ground such as Nosy-Bé (Madagascar - see insert in Figure 2.1, Chapter 2).

CHAPTER 10

Horizontal Trends in Larval Fish Abundance from the Nearshore Coastal Zone to Estuarine Habitat in the St Lucia Region



10. HORIZONTAL TRENDS IN LARVAL FISH ABUNDANCE FROM THE NEARSHORE COASTAL ZONE TO THE ESTUARINE HABITAT IN THE ST LUCIA REGION

10.1. Introduction

To further our understanding of recruitment mechanisms and variability of recruitment of fish larvae from nearshore coastal zones to estuarine nursery areas, studies have examined physical processes in relation to larval transport (Norcross and Shaw 1984; Shaw *et al.* 1985; Koutsikopoulos *et al.* 1991), density distributions, length frequency data and growth rates (Shaw *et al.* 1985, 1988) and vertical distribution patterns of larval fish in relation to environmental factors (Norcross 1991). Both passive and active mechanisms are involved in the recruitment process of larval and juvenile fishes to estuarine nursery areas with environmental factors, such as temperature, salinity, turbidity and current being correlated to the recruitment response (Norcross and Shaw 1984; Boehlert and Mundy 1988; Miller 1988). The ecological coupling or linkage of larval and juvenile fish recruitment between the nearshore zone and estuarine nurseries is referred to as 'ocean-estuarine coupling' of ichthyofauna by Shaw *et al* (1988) and involves a combination of abiotic and biotic factors (Norcross and Shaw 1984).

Once the larvae of estuarine-associated fish species are in the estuarine nursery habitat, the retention of those larvae in the system is important for successful recruitment to take place. Twenty-four hour studies in the entrance channels of estuarine nursery areas have shown that the larvae generally enter the estuarine habitat on night flood tides (Weinstein *et al.* 1980; Rijnsdorp *et al.* 1985; Miskiewicz 1987; Boehlert and Mundy 1987; Drake and Arias 1991; Shenker *et al.* 1993), and on ebb tides larvae of certain species stay in bottom waters to avoid being swept out of the system (Weinstein *et al.* 1980; Melville-Smith and Wooldridge 1981; Robison 1985; Rijnsdorp *et al.* 1985; Roper 1986; Laprise and Dodson 1989; Rowe and Epifanio 1994). This mechanism of retention is otherwise known as selective tidal stream transport (Boehlert and Mundy 1988). In shallow (1 to 3 m), well-mixed entrance channels, vertical movements of larvae are not possible and so to avoid being swept out to sea active movement of larvae to the banks/edges of the channel on the ebb tide occurs

(Beckley 1985a; Whitfield 1989b; Raynie and Shaw 1994) where tidal currents are reduced.

To assess the relative importance of an estuarine nursery habitat, a comparison of the ichthyofaunal communities in the estuary, adjacent surf zone and nearshore marine environment is needed. The restriction of a species in only one habitat implies dependence on the habitat (Lasiak 1981; Blaber *et al.*1989; Potter *et al.* 1990). Juvenile and adult fish communities of tropical estuarine and inshore habitats in northern Australia have different community structures, despite having species common to both habitats (Blaber *et al.* 1994). These differences were attributed mainly to differences in current speed and turbidity. Larval fish assemblages near Indo-Pacific coral reefs are strongly determined by habitat type (Leis 1993). The latter two studies used the multivariate methods of classification and ordination (MDS) to distinguish assemblage patterns.

By examining the structure of larval fish assemblages and the associated environmental factors, along an ocean-estuarine gradient, one can gain insight into factors influencing abundance patterns and possible recruitment mechanisms of larval fish. Chapters 6, 8 and 9 describe the larval fish assemblages in the nearshore coastal zone, surf zone and estuarine habitat, respectively, in the St Lucia region. The present Chapter compares the assemblages of fish larvae from all three habitats and relates the patterns of abundance to the environmental characteristics of each habitat type, by the use of multivariate methods. In addition, two 24 hr studies in the entrance channel of the St Lucia Estuary were undertaken to investigate tidal exchange of larvae and possible mechanisms of recruitment and retention of estuarine-associated fish larvae into the estuary.

10.2 Materials and Methods

10.2.1 Analyses of Data

Larval fish density data from the St Lucia Estuary and adjacent surf and nearshore zones were used in the analyses (Chapters 6, 8 and 9). To recap, densities of all species, from each estuarine system, were standardised to number of larvae per $100m^3$ (see section 3.2.2, Chapter 3). These data were then placed in a matrix with species as rows and

samples as columns (374 species over 36 months, Appendix VII). As with the analyses in Chapter 7, the matrix becomes too large if all samples taken each mouth at each site are used (312 for St Lucia Estuary; 144 for the surf zone, and 396 for the nearshore study i.e. total samples = 852). Therefore, the mean monthly densities of each species at each location were used as the samples. Using mean monthly values has the advantage of simplifying large data sets with little loss of information and identifying interrelations among variables (Morais and Morais 1994). For the environmental data matrix, mean monthly values of salinity, temperature and turbidity were used.

The software program used for all the analyses was PRIMER v3.1b (Plymouth Routines in Multivariate Ecological Research) devised by Clarke and Warwick (1994), in addition to the methods of Field *et al.* (1982). The data were analysed using univariate, graphical and multivariate analyses in the following way:

1.) Species diversity and evenness

Shannon-Wiener's Diversity Index: $H' = -\sum_i p_i (\log p_i)$

Pielou's Evenness Index: $J' = H'$ (observed)$/H'_{max}$

2) Graphical/distributional

Dominance curves - based on the ranking of species in decreasing order of their importance in terms of abundance. The ranked abundances are plotted against the logged species rank (logging the x-axis enables the distribution of commoner species to be better visualised). Cumulative or K-dominance curves are the ranked abundances plotted against log species rank where the most elevated curve has the lowest diversity.

3) Classification

Biotic data - hierarchical agglomerative clustering with group-averaging linking, based on the Bray-Curtis Similarity measure (ranked) was used to delineate groups with distinct community structure. Abundance values were root-root

transformed for the analysis. The root-root transformation down-weights the more abundant species and is invariant to scale change (Field *et al.* 1982). Two types of classification analyses were done :

- by site using all species
- by species (inverse analysis) using only the top 20 ranked species from each site (see Tables 6.1, 8.1 and 9.1) i.e. total of 47 dominant species. Indicator species at each site could then be identified using the program SIMPER which examines the contribution of individual species to the similarity measure used.

Abiotic data - environmental variables were log transformed [log10 (x + 1)], where necessary, to conform to normality. Hierarchical agglomerative clustering with group-averaging linking, based on the Normalised Euclidean Distance Dissimilarity measure (ranked) was used to delineate groups.

4) Ordination

Non-metric multidimensional scaling (MDS) was used where a stress level of <0.20 gives an adequate representation of the 2-dimentional MDS. At least 10 runs were done to find the global minimum i.e. runs are done until two or more solutions with the same stress value in achieved.

5) BIO-ENV procedure

This relates the biotic to the abiotic factors by superimposing the environmental data on the biotic ordination i.e. links the community data to the environmental variables. The premise here is that if a suite of environmental variables is responsible for structuring the community, the abiotic ordination would be similar to the biotic groupings (Clarke and Warwick 1994). From the MDS plots one can determine which environmental variables are influencing the community structure.

6) Significance tests

For discrimination between sites, one-way ANOVA was used for the diversity and evenness indices (95% Confidence limit). The non-parametric weighted Spearmans (or harmonic) rank correlation (ρ_w) was used to test the correlations between the biotic and abiotic similarity matrices determined from the BIO-ENV procedure. In addition, the relationship between biotic and abiotic factors was analysed by a correlation matrix - correlation coefficients for the 15 abundant species (density data) for all three systems were calculated for each environmental variable. The mean monthly values were (n = 36) from all three sites together .

10.2.2 24-h Inlet Study

Refer to section 2.4.2 (pg.15) for description of the study area. The collection of fish larvae is described in section 3.1.2.2 (pg. 22), and the laboratory procedures are the same as for all the other studies (section 3.2, Chapter 3).

10.3 Results

10.3.1 Composition of the Larval Fish Assemblages

A summary of the abiotic and biotic characteristics of each zone from nearshore to estuarine habitat is given in Table 10.1. The estuarine habitat is distinct from the surf and nearshore zones by having a wider range in environmental values. The composition of the larval fish assemblages differed in each habitat with the dominant families and species in the nearshore zone being predominantly estuarine-independent species and in the estuarine environment predominantly estuarine-dependent species. The surf zone was occupied by a combination of estuarine-dependent, partially estuarine-dependent and surf resident species (e.g. *P.olivaceum*). The main recruitment period is influenced by the dominant species prevailing in each environment. The larvae in the nearshore zone were mainly at preflexion and flexion developmental stages, whilst in the surf zone and estuary mainly postflexion larvae were present. Salinity,

Table 10.1. Summary of abiotic and biotic characteristics of the nearshore, surf and estuarine habitats in St Lucia.

	Nearshore	Surf zone	Estuary
Physical structure	open sea	wave action	completely sheltered
Environmental variables (min-max)			
Salinity (‰)	28.0-36.0	33.0-36.0	1.0-36.0
Temperature (°C)	18.0-27.0	18.8-28.8	17.5-30.5
Turbidity (NTU)	0.5-328	0.0-48.9	10.2-755.0
Dominant families (% of total catch)	Myctophidae (21%) Tripterygiidae (16%) Clupeidae (7%)	Sparidae (20%) Haemulidae (16%) Ambassidae (10%)	Gobiidae (75%) Clupeidae (19%) Engraulidae (2%)
Dominant species	Tripterygiid 1 *B.fibulatum* *E.teres*	*P.olivaceum* *Ambassis* sp. *R.holubi*	*G.callidus* *G.aestuaria* *C.massambica*
Estuarine-association (% of total density)			
Estuarine dependent	0.8	19.9	25.2
Partially estuarine dependent	9.2	46.6	74.1
Estuarine independent	90.0	33.5	0.7
Main recruitment period			
Estuarine dependent	early summer, autumn	late winter	autumn
Partially estuarine dependent	late spring, autumn	autumn	late spring, summer
Estuarine independent	late spring, early summer	late spring	autumn, winter
Developmental stages (% of total catch)			
Estuarine dependent			
Young (Pr,Fl)	0.3	0.1	8.9
Old (Po)	0.4	21.7	12.1
Partially estuarine dependent			
Young (Pr,Fl)	3.3	0.3	1.8
Old (Po)	5.8	46.3	76.5
Estuarine independent			
Young (Pr,Fl)	66.7	2.6	0.2
Old (Po)	23.5	29	0.5
Significant variables (% contribution to regression model)[A]			
Estuarine dependent	———	tu (4%)	tu,-sa (45%)
Partially estuarine dependent	tu,sa (3%)	tu (9%)	tu,te (29%)
Estuarine independent	-te,sa (10%)	———	sa,te,cu (8%)

[A]sa, salinity; te, temperature; tu, turbidity

temperature and turbidity only accounted for a small amount of the variability in larval densities in the nearshore and surf zone, but did account for a large proportion of variability in the estuarine habitat (Table 10.1).

The mean species diversity index was significantly higher in the nearshore zone (H' = 1.36; F = 23.85, P < 0.0001) than both the surf zone (H' = 0.81) and the estuary (H' = 0.68). Both the surf and nearshore zone had significantly higher evenness values (J' = 0.66 and 0.7, respectively, P = 0.008) than the estuarine habitat (J' = 0.47). The patterns of relative species abundances in each habitat (K-dominance curves) showed that the estuarine environment is dominated by a few species in large numbers, the surf zone is intermediate, and the nearshore zone is the most diverse (Figure 10.1).

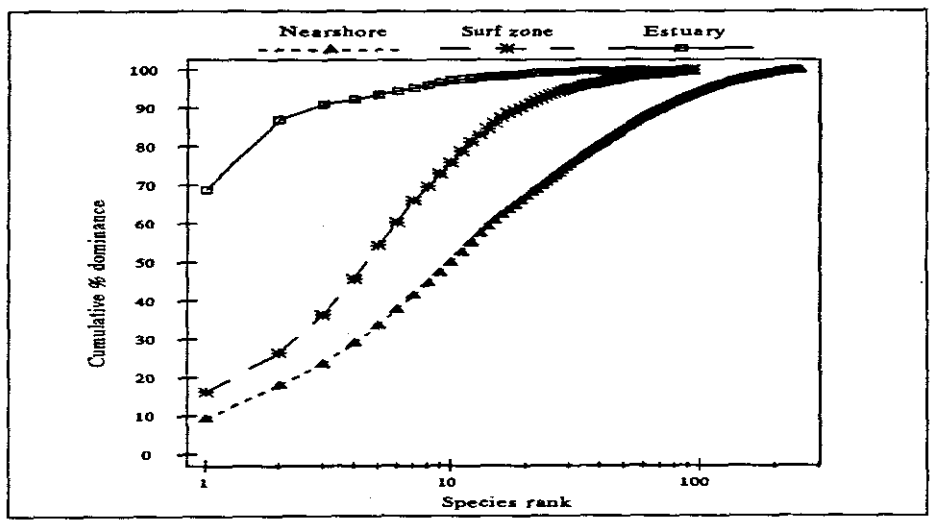


Figure 10.1. K-dominance curves for species abundance data from the St Lucia Estuary and the adjacent surf and nearshore habitats. (Note: the x-axis is on a log scale).

Classification and ordination analyses of larval densities from all three habitats separated out into three main groups at the 15% similarity level (Figure 10.2A and B). Group 1 consisted of all the estuary samples, Group 2 all the surf samples and Group 3 all the nearshore samples (stress level = 0.12).

The species similarity matrix (inverse analysis) clusters into four main groups at the 10% similarity level and seven subgroups at the 15% similarity level (Figure 10.3A). The ordination (MDS) of the same similarity matrix (stress level = 0.24) shows that the dominant species separated out according the degree of estuarine association of a species

and hence habitat zone (Figure 10.3B). Table 10.2 summarises the species groups distinguished by the inverse analysis: Group 1 is an outlier and is an unidentified scombrid abundant in the nearshore zone. Group 2 has two subgroups: Group 2a is a goby species, *G.callidus*, which spawns in freshwater and in estuaries and is therefore partially dependent on estuaries; Group 2b consists of estuarine-associated species found only in the estuary or both the estuary and the surf zone, except for *S.holodon* which was in all three habitat areas. Group 3 also has two subgroups: Group 3a is two pelagic species, *H.quadrimaculatus* (estuarine-dependent) and *C.chanos* (partially estuarine-dependent), found in the surf zone and nearshore zone; Group 3b is predominantly partially estuarine-dependent species abundant in the estuary and/or surf zone. Group 4 is mainly estuarine independent species with two subgroups: Group 4a consisted of all three unidentified tripterygiid species and a gobiesocid, *Lepadichthys* sp.2, which are all reef-associated taxa; Group 4b is a combination of pelagic, reef and oceanic-associated taxa with the soapy, *L.equula*, being the only estuarine-associated species in this group. In summary, most species are strongly related to site groups, although some species are common to two or all three habitat areas. The species contributing most to the site groupings (derived from SIMPER analysis) are underlined in Table 10.2.

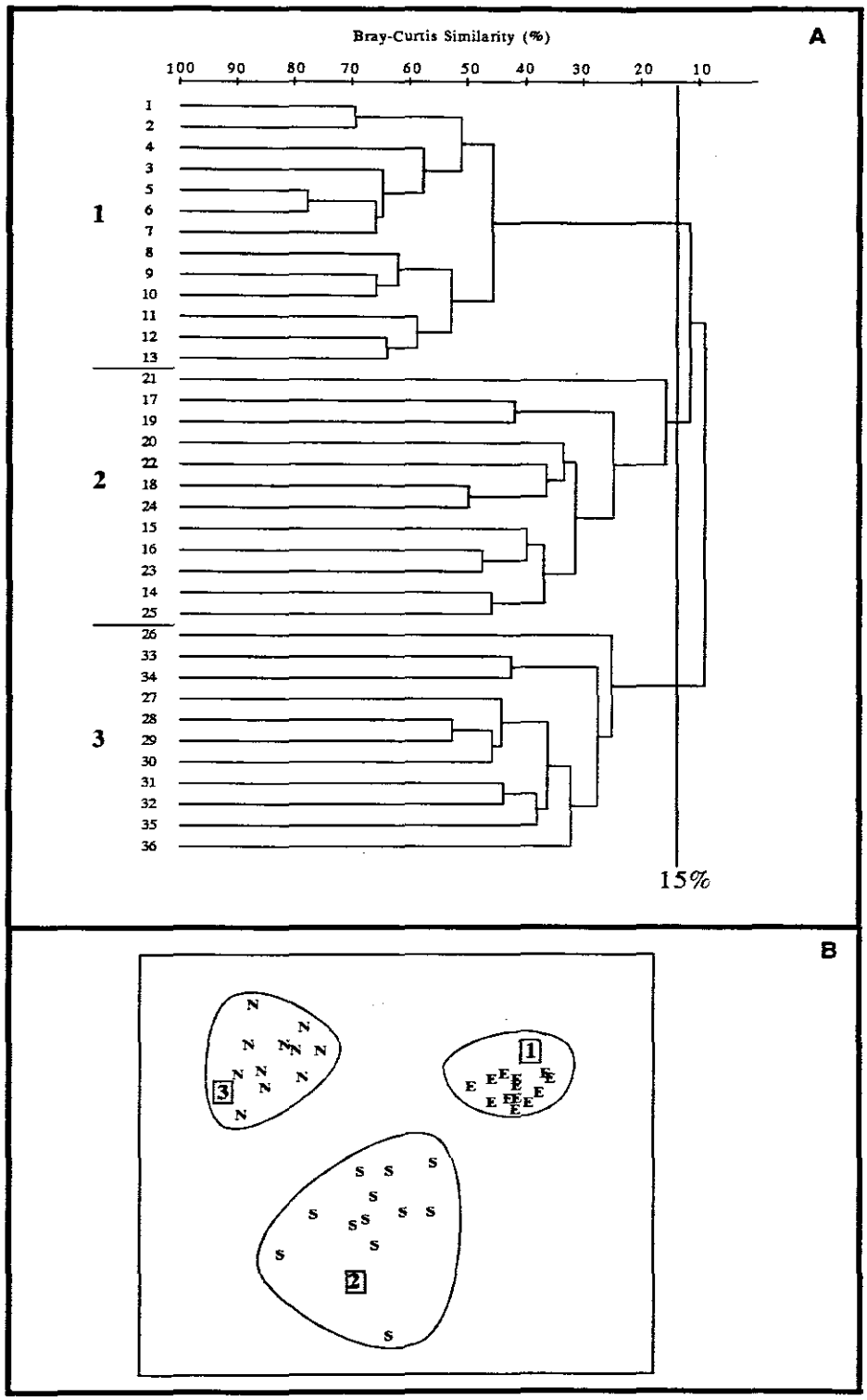


Figure 10.2. Dendrogram (A) showing the clustering of the three habitats (E, St Lucia Estuary; S, surf zone; N, nearshore shelf waters) based on mean monthly abundances, and the ordination in 2-dimensions (B) using MDS on the same similarity matrix. Clusters 1 to 3 were distinguished from the dendrogram (A) and are indicated by circles in the ordination (B).

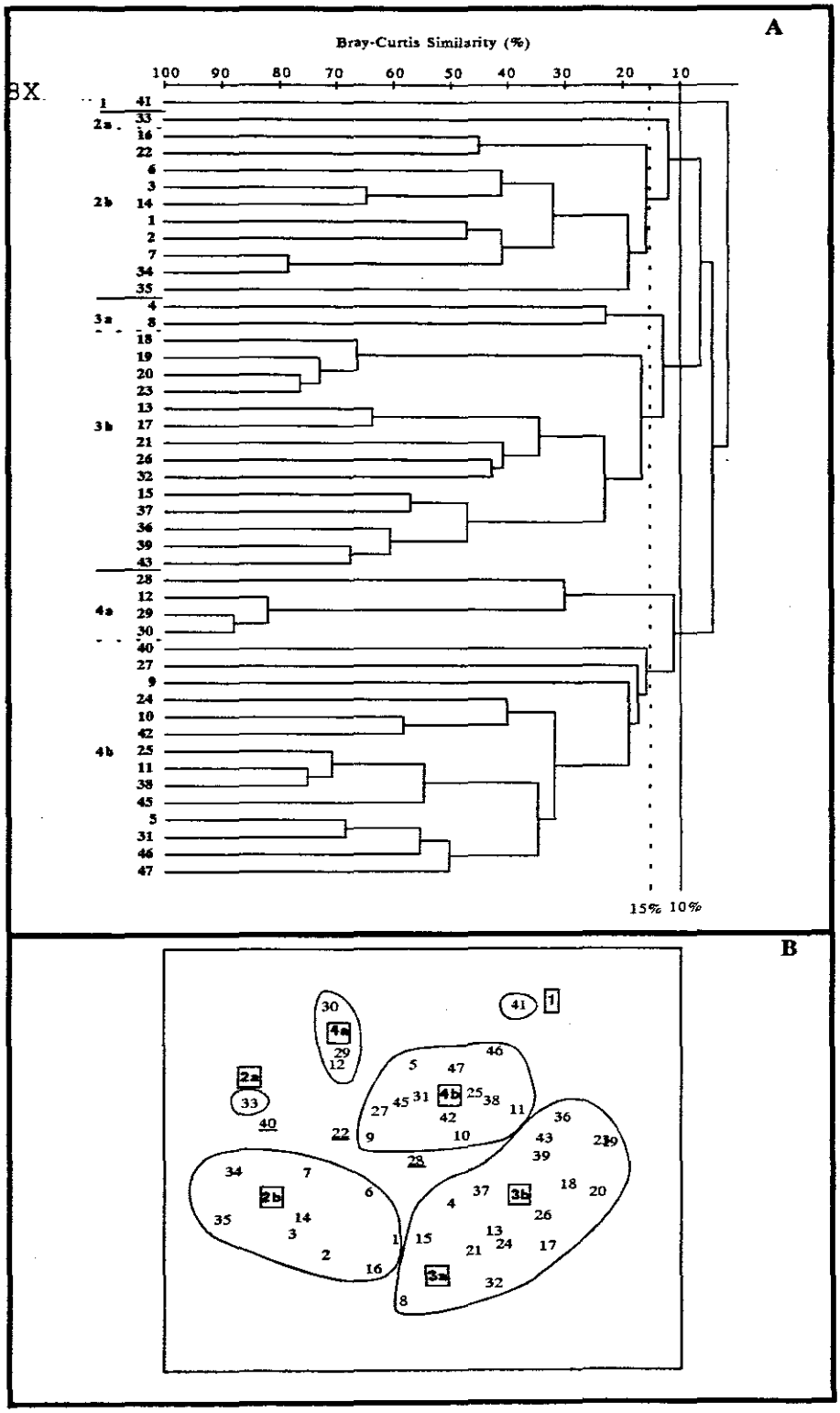


Figure 10.3. Dendrogram (A) showing the inverse analysis clustering based on mean monthly abundances of 47 species occurring in the top 20 ranked species from each habitat, and the ordination in 2-dimensions (B) using MDS on the same similarity matrix. Clusters 1 to 4 and subclusters 2a, 2b, 3a, 3b, 4a and 4b were distinguished from the dendrogram (A) and are indicated by circles in the ordination (B).

Table 10.2. Species groups distinguished by inverse analysis. Species numbers refer to those in both the classification and ordination diagrams (Figure 10.3) derived from the dominant species matrix (species underlined = species contributing most to similarities in a group)

Group	Species code no.[A]	Species	Est-assoc group[B]	Habitat[C]
Group 1	41	Scombrid 2	indep	nearshore
Group 2a	33	*Glossogobius callidus*	part-dep	estuary
Group 2b	16	*Terapon jarbua*	est-dep	estuary/surf
	22	*Gerres* sp.1	part-dep	surf
	6	*Stolephorus holodon*	part-dep	estuary/surf/nearshore
	3	*Gilchristella aestuaria*	est dep	estuary
	14	*Hippichthys heptagonus*	part-dep	estuary
	1	*Elops machnata*	est-dep	estuary/surf
	2	*Megalops cyprinoides*	est-dep	estuary
	7	*Thryssa vitrirostris*	est-dep	estuary
	34	*Redigobius* sp.	est-dep	estuary
	35	*Taenioides esquivel*	part-dep	estuary
Group 3a	4	*Herklotsichthys quadrimaculatus*	indep	surf/nearshore
	8	*Chanos chanos*	part-dep	surf
Group 3b	18	*Rhabdosargus holubi*	est-dep	estuary/surf
	19	*Diplodus sargus capensis*	indep	surf
	20	*Acanthopagrus berda*	est-dep	surf
	23	*Johnius dussumieri*	part-dep	estuary
	13	*Iso natalensis*	indep	surf
	17	*Pomadasys olivaceum*	indep	surf
	21	*Monodactylus argenteus*	part-dep	surf
	26	Mugilid spp.	part-dep	surf
	32	*Croilia mossambica*	part-dep	estuary/surf
	15	*Ambassis* sp.	part-dep	estuary/surf
	37	Gobiid 1	part-dep	surf
	36	*Taenioides jacksoni*	est-dep	estuary
	39	Eleotrid 2	est-dep	estuary/surf
	43	*Solea bleekeri*	part-dep	estuary/surf
Group 4a	28	Tripterygiid 1	indep	nearshore-reef
	12	*Lepadichthys* sp.2	indep	nearshore-reef
	29	Triptergyiid 2	indep	nearshore-reef
	30	Tripterygiid 3	indep	nearshore-reef
Group 4b	40	*Rastrelliger kanagurta*	indep	nearshore-pelagic
	27	Blenniid 6	indep	nearshore-reef
	9	*Vinciguerria attenuata*	indep	nearshore-oceanic
	24	*Leiognathus equula*	part-dep	estuary/nearshore
	10	*Bregmaceros atlanticus*	indep	nearshore-pelagic
	42	*Engyprosopon grandisquama*	indep	nearshore-reef
	25	*Secutor insidiator*	indep	nearshore-reef
	11	*Bregmaceros nectabanus*	indep	nearshore-reef
	38	Gobiid 4	indep	nearshore-reef
	45	*Benthosema pterotum*	indep	nearshore-oceanic
	5	*Etrumeus teres*	indep	nearshore-pelagic
	31	*Draculo celatus*	indep	nearshore-reef
	46	*Benthosema fibulatum*	indep	nearshore-oceanic
	47	*Diogenichthys pangurgus*	indep	nearshore-oceanic

[A]species code numbers derived from classification and ordination (Fig. 10.3)

[B]estuarine-association group:est dep, estuarine-independent; part dep, partially estuarine-dependent; indep, estuarine-independent.

[C]Habitat where each species was present - for the dominant species matrix only

10.3.2 Relationship of Habitat Groups to Environmental Variables

Figure 10.4. represents the same habitat groups from Figure 10.2B with the environmental variables, salinity, temperature and turbidity, superimposed on the habitat samples. The estuarine habitat is characterised by low to high salinities and temperatures, and high turbidities. The nearshore marine environment and the surf zone had similar salinities and temperatures but different turbidities.

The ordination for the environmental data indicated that a gradient in environmental conditions existed from nearshore to estuarine habitat (Figure 10.5). Turbidity was the main environmental variable explaining the observed community patterns (weighted Spearman's ranked correlation, ρ_w = 0.39). However, different combinations of the environment variables were also correlated to community structure to some degree. For example, salinity + turbidity (ρ_w = 0.33) and temperature + turbidity (ρ_w = 0.24) (Figure 10.5).

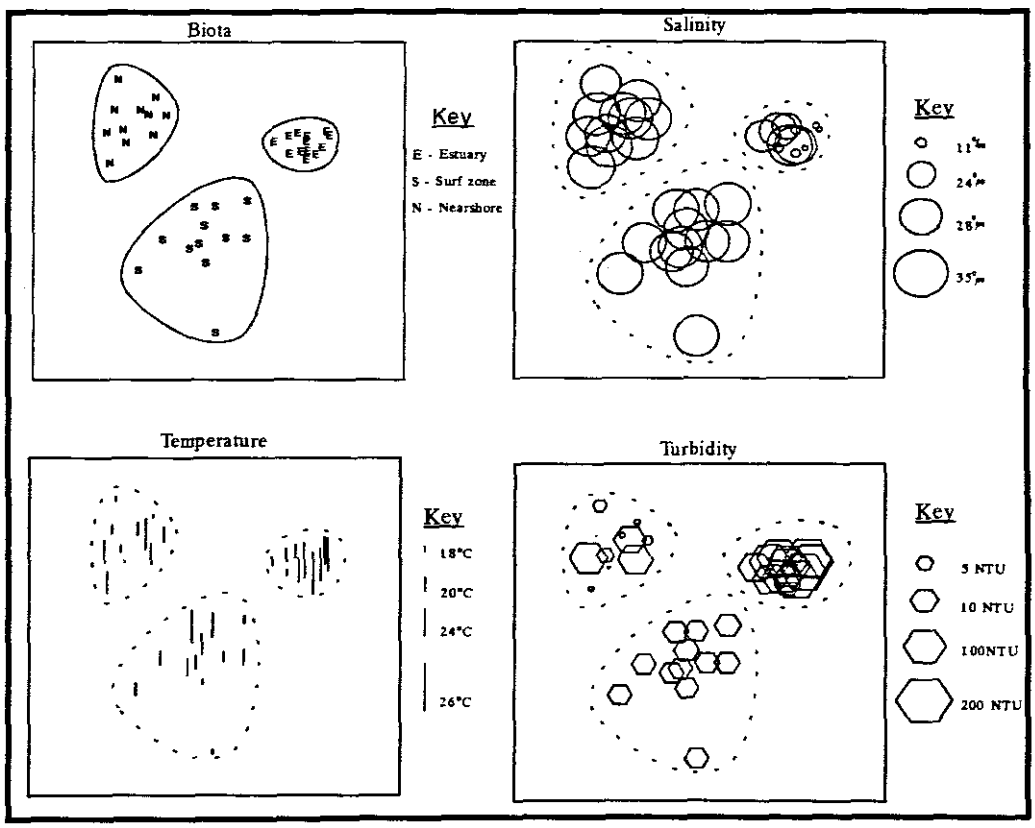


Figure 10.4. MDS of species abundances in the three habitats (A) (E, St Lucia Estuary; S, surf zone; N, nearshore marine environment). (B) - (D) are the same MDS but with superimposed symbols representing salinity, temperature and turbidity mean monthly values at each site.

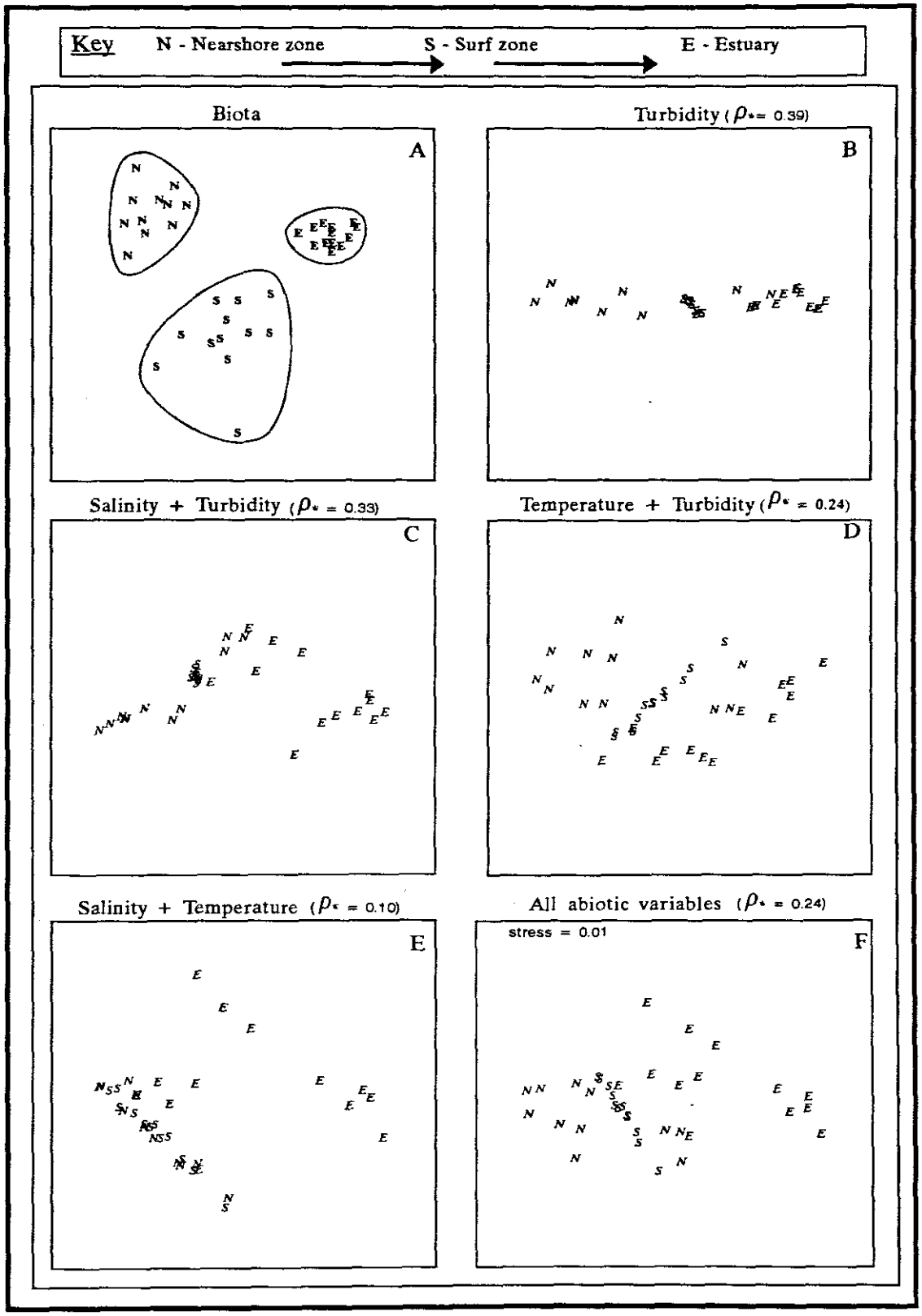


Figure 10.5. MDS ordinations of the three habitats (E, St Lucia Estuary; S, surf zone; N, nearshore marine environment) on (A) species abundances, (B) turbidity, (C) salinity + turbidity, (D) temperature + turbidity, (D) salinity + temperature, (E) all abiotic variables.

The relationship of larval densities to the environmental variables was shown to species-specific. Densities of the 15 most abundant species from all three areas were correlated to different abiotic variables (Table 10.3).

Table 10.3. Correlation coefficients (R) between 16 abundant species and the environmental variables. (95% confidence limits).

Species abbreviation[A]	Species	Salinity (‰)	Temperature (°C)	Turbidity (NTU)
G.c	*Glossogobius callidus*	-0.89***	0.57***	0.71***
G.a	*Gilchristella aestuaria*	-0.86	0.51***	0.66***
T.j	*Taenioides jacksoni*	-0.79***	0.35*	0.74***
P.o	*Pomadasys olivaceum*	0.22	-0.07	-0.07
T1	Tripterygiid 1	0.37*	-0.27	-0.46*
Am	*Ambassis* sp.	-0.21	0.27	0.34*
E.m	*Elops machnata*	-0.43*	0.22	0.44*
S.h	*Stolephorus holodon*	-0.37*	0.23	0.51**
T.v	*Thryssa vitrirostris*	-0.50**	0.55**	0.50**
R.h	*Rhabdosargus holubi*	0.22	-0.02	-0.08
C.c	*Chanos chanos*	0.16	0.14	0.07
Rg	*Redigobius* sp.	0.38*	0.57***	0.38*
S.b	*Solea bleekeri*	-0.27	-0.18	0.20
B.f	*Benthosema fibulatum*	0.16	-0.26	-0.39*
D.s	*Diplodus sargus capensis*	0.16	-0.28	-0.06

[A]Species abbreviations as shown in Figure 10.6
*P<0.05;**P<0.01; ***P<0.001

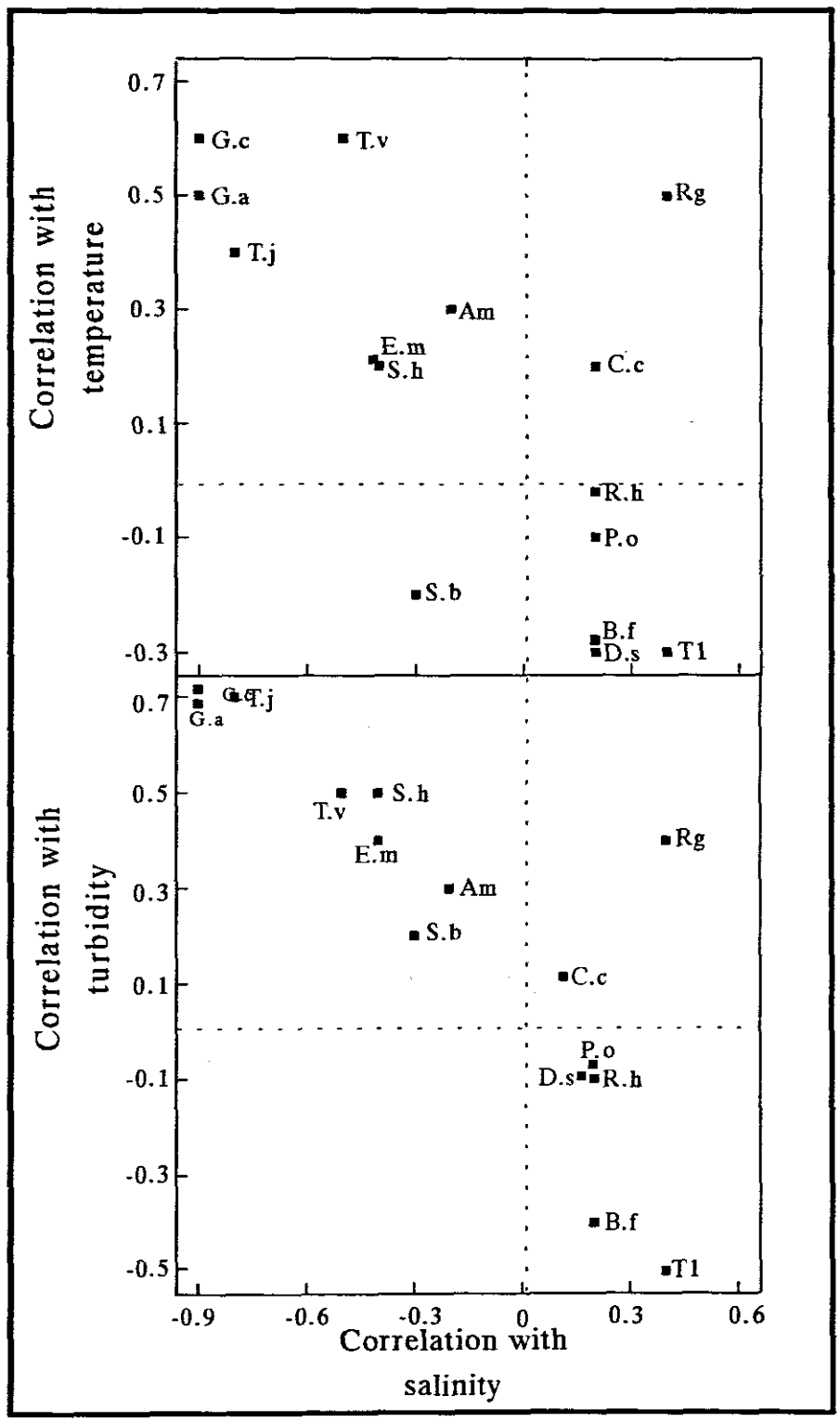


Figure 10.6. Correlation coefficients (R) of larval density vs salinity (x-axis), plotted against correlation coefficient of larval density vs temperature and turbidity (y-axis). Dotted lines indicate 4 quadrants which correspond to habitat type: 1 - estuarine; 2 - semi-estuarine; 3 - semi-marine; 4 - marine. Species abbreviations are explained in Table 10.3.

10.3.3 Tidal Exchange of Fish Larvae

10.3.3.1. Environmental Conditions

Both the February and March 1994 24-h sampling sessions coincided with spring tide conditions on a full moon. During the February sampling session predicted times for low and high tide in Richards Bay (closest place where accurate tide readings available) were 22h26/10h45 and 16h18/04h37, respectively. The range in tidal height was 2.27 m with the depth of the channel station ranging from 1.1 - 3.0 m. The maximum current velocity was 1.6 $m.s^{-1}$ during the day flood period and salinities were essentially marine remaining at 35‰ throughout the sampling session (Figure 10.7). Temperature reached a maximum of 27.7°C and turbidity a maximum of 15 NTU.

During the March sampling session predicted times for low and high tide in Richards Bay were 21h27/09h48 and 15h20/03h38, respectively. The range in tidal height was 2.23 m with the depth of the channel site ranging from 1.5 - 2.5 m. Maximum current velocity was 1.5 $m.s^{-1}$ and salinities remained at 35‰ (Figure 10.8). The maximum temperature and turbidity values were 26.5°C and 30.5 NTU.

For both the February and March sampling sessions, current velocity, salinity and temperature did not differ significantly between ebb and flood tides with only turbidity being significantly higher on ebb tides ($F = 11.2$; $P = 0.001$; $N = 132$). Salinity, turbidity and current velocity did not differ significantly between day and night whereas temperature was significantly higher during the day ($F = 37.9$; $P < 0.0001$; $N = 132$). Since all environmental variables were only measured at the channel site, differences between sites cannot be assessed. However, for current velocities, a current profile across the estuary mouth was undertaken in February 1991, on both the spring flood and ebb tides (see Figure 2.5, Chapter 2). The profile shows that current velocities in the mid-channel site were much higher than at the edges and near the bottom of the channel.

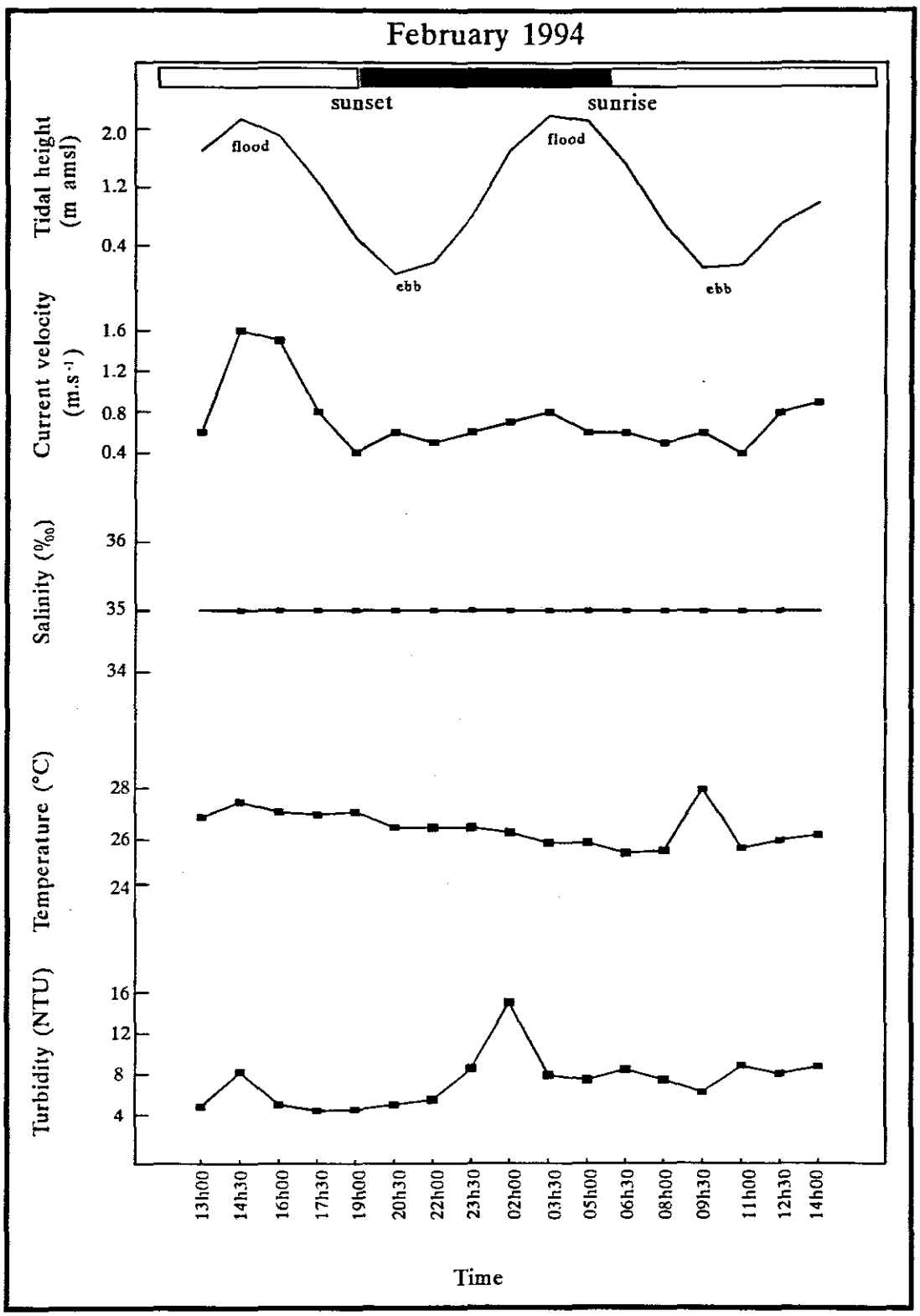


Figure 10.7. Variations in environmental variables (current velocity, salinity, temperature and turbidity) during the February 1994 24-h inlet study. (amsl, average meters above sea level)

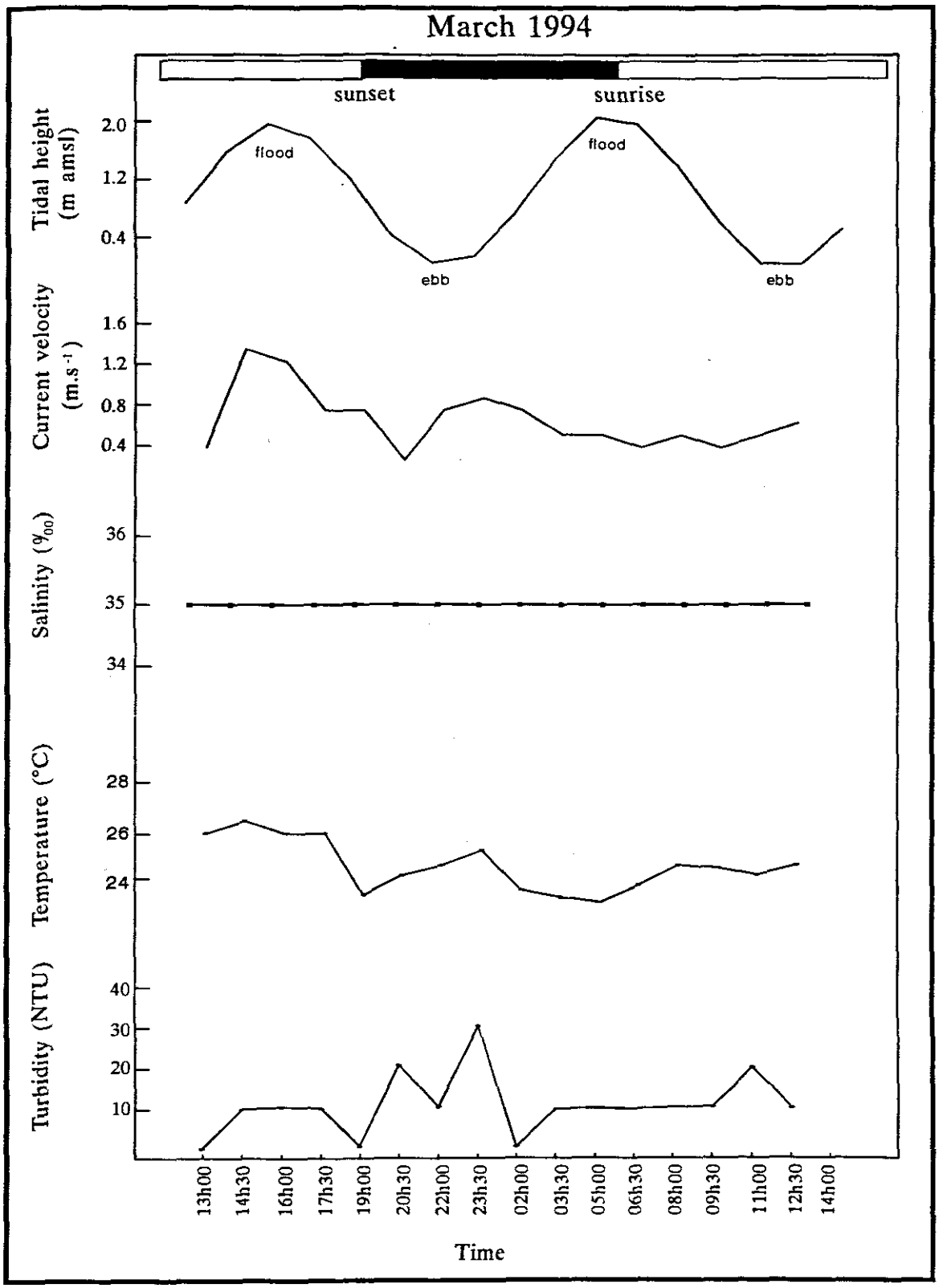


Figure 10.8. Variations in environmental variables (current velocity, salinity, temperature and turbidity) during the March 1994 24-h inlet study. (amsl, average meters above sea level)

10.3.3.2 Species Composition and Estuarine-Association

A total of 5 569 larvae, representing 41 families and 63 taxa, was collected during both the February and March 24-h sessions (Table 10.4). The most abundant species was the goby *C.mossambica*, comprising 20% of the total catch. Other dominant species contributing greater that 2 % of the total catch were, in order of abundance, Gobiid 1 (6.2%), *C.chanos* (5.6%), Eleotrid 1 (2.9%), *S.holodon* (2.8%) and *M.cyprinoides* (2.4%).

Different species predominated in samples taken at the mid-channel site and the channel edge site during each of the tidal periods. These were mainly estuarine-associated species (Table 10.4). At the mid-channel site on ebb tides, very few larvae of only some species were collected during the day (generally only 6.3% of the 16 day ebb samples) with more larvae, particularly *T.jacksoni* and *S.holodon* (> 40% of the 16 night ebb samples), being present in night ebb samples. On flood tides at the mid-channel site, larvae were collected during both day and night periods depending on the species. For example, *C.mossambica,* Gobiid 1 and *T.jacksoni* were present in 50% or more of the 18 day flood samples whilst *C.mossambica,* Gobiid 1 and *S.holodon* were present in 50% or more of the night flood samples. Species abundant in samples at the edge site were *M.cyprinoides*, *E.machnata*, *C.mossambica*, Gobiid 1, *S.holodon* and *C.chanos,* each being present in more than 50% of the samples taken at each tide period (Table 10.4). Most larvae in edge samples were collected at night on both flood and ebb tides. Of the estuarine-associated species, specimens of *G.aestuaria, R.sarba, Monodactylus argenteus,* Mugilid spp., *A.gymnocephalus*, *T.esquivel, Gerres* sp.2 and *Sphyraena jello* were only collected in edge samples.

Of the 63 taxa recorded, 26 species were estuarine-associated (43.6% of the total catch) and 33 species were estuarine independent (56.4% of the total catch) (Figure 10.9). One freshwater species (*Microphis fluviatilis)* and one oceanic species (*Benthosema pterotum*) were collected on the flood tide (Table 10.4). Partially estuarine-dependent species were particularly abundant comprising 78.2% of the total density, with estuarine-dependent species also being relatively abundant (17.2% of total density; Figure 10.9). Only 3.6% of the total density was attributed to estuarine independent taxa.

Table 10.4. Percentage occurrence, body lenth and developmental stage for all species during each tidal period at the two sites in the mouth of the St Lucia Estuary. Tides: DF, day flood; DE,day ebb; NF, night flood; NE, night ebb (n = number of samples taken on that tide). Presence: presence in the February (F) and March (M) 24-h sampling sessions. (*abundant; **very abundant)

			Mid-channel						Edge							
Family	Species	Overall Rank	DF n = 18 (%)	DE n = 16 (%)	NF n = 16 (%)	NE n = 16 (%)	Total caught (no.)	Mean size (range) (mm)	DF n = 20 (%)	DE n = 16 (%)	NF n = 14 (%)	NE n = 16 (%)	Total caught (no)	Mean size (range) (mm)	Developmental stages	Presence
ESTUARINE-DEPENDENT																
Estuarine residents																
Clupeidae	*Gilchristella aestuaria*											6.3	1	29	Ju	M
Gobiidae	*Omobranchus woodi*			6.3			1	8				6.3	1	15	Po	F,M
	Psammogobius knysnaensis		5.56		6.3		2	6.5(6.4-6.6)			14.3		3	6.5(6-7)	Po	F
	Redigobius sp.					6.3	3	2.5			7.1		7		Pr	F
	Taenioides jacksoni	7	50.00		25.0	50.0	52	9.3(8-10)	20.0	12.5	35.7	37.5	74	9.2(9-10)	Po	F,M*
Eleotridae	Eleotrid 2	4	16.67	6.3	31.3	18.8	56	15.0(14-16)		31.3	14.3	31.3	106	14.5(10-15.5)	Po	F,M*
Marine spawners dependent on estuaries																
Elopidae	*Elops machnata*	8	5.56		18.8	12.5	11	31.2(28-34)	15.0	25.0	21.4	56.3	48	29.3(22-36)	Le	F,M*
Engraulidae	*Thryssa vitrirostris*		16.67		12.5	25.0	15	7.0(4.5-9)				6.3	1	7.5	Pr,Fl,Po	F,M*
Teraponidae	*Terapon jarbua*	10	11.11		12.5	6.3	5	9.5(7-11)		12.5	42.9	18.8	42	10.5(10-12)	Po	F,M*
Haemulidae	*Pomadasys commersonnii*	9	5.56				3	12			28.6	6.3	52	12.1(11-14)	Po	M
Sparidae	*Rhabdosargus sarba*									12.5			2	10	Po	M
Monodactylidae	*Monodactylus argenteus*										28.6		7	4.9(4.8-5)	Po	M
Leiognathidae	*Leiognathus equula*		16.67		37.5	18.8	15	9.4(3-42)							Pr,Fl,Ju	F,M
PARTIALLY ESTUARINE-DEPENDENT																
Catadromous																
Megalopidae	*Megalops cyprinoides*	6	16.67		37.5	25.0	35	24.3(16-29)	30.0	50.0	21.4	43.8	96	23.5(19.3)	Le	F,M*
Estuarine and marine spawners																
Syngnathidae	*Hippichthys heptagonus*			6.3		12.5	4	9.8(7-18)		6.3			1		Po,Ju	F,M
Ambassidae	*Ambassis gymnocephalus*								5.0		14.3	12.5	10	40.1(35-48)	Ju	F,M*
	Ambassis sp.		5.56		6.3	6.3	3	4.9(4-5.8)		6.3	14.3	31.3	30	5.9(4-8)	Po	F,M*
Gobiidae	*Croilia mossambica*	1	55.56	6.3	56.3	25.0	257	10.8(8-14)	10.0	12.5	50.0	25.0	878	10.8(7-12)	Po	F,M**
	Taenioides esquivel								10.0					9.2(6-11)	Po	F,M
	Gobiid 1	2	55.56	6.3	50.0	37.5	131	5.7(3-7.5)		6.3	64.3	43.8	212	5.7(5-7)	Fl,Po	F,M**
Marine spawners with juvenilesmabundant in estuaries																
Soleidae	*Solea bleekeri*		16.67		18.8		12	3.4(7.8-4)			14.3		11	3.3(3-3.5)	Po,Ju	F,M*
Mugilidae	Mugilid spp.								10.0	12.5	14.3	25.0	42	15.9(11-25)	Po,Ju	F,M*
Marine spawners with juveniles at sea and in estuaries																
Engraulidae	*Stolephorus holodon*	5	11.11	12.5	56.3	43.8	79	17.3(8-32)	15.0	50.0	7.1	62.5	74	19.2(5-50)	Pr,Fl,Po,Ju	F,M*
Chanidae	*Chanos chanos*	3	5.56	6.3	31.3	6.3	23	12(11-17)	35.0	31.3	57.1	31.3	288	11.4(10-13)	Po	F,M**
Gerreidae	*Gerres sp.1*			6.3		6.3	2	9		12.5			9	8.8(8-10)	Po	M
	Gerres sp.2										14.3		2	15.5(14-17)	Po	M
Sillaginidae	*Sillago sihama*			6.3	6.3		2	9.3(6.5-12)				12.5	2	14(13-15)	Po	M
Sphyraenidae	*Sphyraena jello*											6.3	1	27	Po	M
Gobiidae	Gobiid 5			6.3	12.5	18.8	7	8.4(7.2-11.5)			21.4		6	10.2(7-11)	Po	F,M*
	Gobiid 13					12.5	11	2.6(1.5-3)	5.0	6.3			2	2.8	Pr	F,M

cont.

Table 10.x continued

Family	Species	Overall Rank	Mid-channel DF n = 18 (%)	Mid-channel DE n = 16 (%)	Mid-channel NF n = 16 (%)	Mid-channel NE n = 16 (%)	Mid-channel Total caught (no.)	Mid-channel Mean size (range) (mm)	Edge DF n = 20 (%)	Edge DE n = 16 (%)	Edge NF n = 14 (%)	Edge NE n = 16 (%)	Edge Total caught (no.)	Edge Mean size (range) (mm)	Developmental stages	Presence
	ESTUARINE INDEPENDENT															
	Freshwater															
Syngnathidae	*Microphis fluviatilis*						1	79							Ju	M
	Reef and shore taxa															
Muraenidae	*Thrysoidea macrura*		16.67	6.3	12.5	18.8	16	91.3(80-103)	10.0	6.3	7.1	6.3	13	90.1(76-100)	Le	F,M*
Opichthidae	*Opichthus sp.1*				6.3		1	76				6.3	1	68	Gl	M
	Opichthid 1					6.3	1	91							Le	F
Muraenisocidae	*Muraenasax bagio*		11.11			6.3	3	86.3(83-90)							Le	F,M
Clupeidae	*Herklotsichthys quadrimaculatus*		11.11		18.8	18.8	10	7.5(3.8-11)	5.0				2	11(10-12)	Pr,Fl,Po	F,M
Engraulidae	*Thryssa setirostris*				6.3		1	36		6.3		12.5	4	31.3(29-32)	Ju	F,M
Chirocentridae	*Chirocentrus dorab*		5.56				1	11							Fl	F
Antennariidae	*Histrio histrio*				6.3		1	7							Po	M
Gobiesocidae	*Lepadichthys sp.2*									6.3			2		Po	M
Haemulidae	*Plectorhinchus* sp.1											6.3	1	8	Po	M
Lutjanidae	*Lutjanus argentimaculatus*				6.3		2	16.5(16-17)			28.6		9	17.2(14-24)	Po	F,M*
Sparidae	Sparid 4				6.3		1	4.2							Fl	M
Nemipteridae	*Nemipterus sp.*				6.3		1	4							Fl	F
Scorpididae	*Neoscorpis lithophilus*		5.56				1	14			7.1		2	10.5(10-11)	Po	F,M
Mullidae	Mullid 1		5.56				1	4				6.3	1	5	Fl,Po	F
Carangidae	*Caranx* sp.								5.0				1	42	Ju	M
Pempheridae	*Pempheris* sp.1				6.3		1	5.8				6.3	1	5	Fl,Po	M
Pomacentridae	*Abudefduf* sp.		5.56				1	6.5		6.3		6.3	2	12(11-13)	Po	F,M
Labridae	Labrid 1											6.3	1	9	Po	F
	Labrid 7											6.3	1	8	Po	M
Scaridae	*Scarus sp.*		5.56			6.3	2	5.8(4-7.5)							Pr,Po	F,M
Polynemidae	*Polydactylus plebius*										7.1		1	32	Ju	M
Trichonotidae	*Trichonotus marleyi*					6.3	1	14			7.1		1	10	Po	M
Blenniidae	Blenniid 1					31.3	6	2.3(2-2.8)	5.0			6.3	3	5.4(2.8-7)	Pr,Fl,Po	F,M
Tripterygiidae	Tripterygiid 1		5.56				2	3.5(3-4)		6.3			1	4.8	Pr,Fl	F,M
Gobiidae	Gobiid 7					6.3	1	5			7.1	6.3	5	13.3(12-14)	Po	M
	Gobiid 8					6.3	1	11				6.3	4		Po	M
Bothidae	*Engyprosopon grandisquama*				6.3		1	8.5				6.3	1	8	Po	F
Monacanthidae	*Stephanolepis auratus*					6.3	1	19.5	5.0				1	21	Po,Ju	F
Tetraodontidae	*Arothron immaculatus*										14.3		6	10.4(10-11.5)	Po	M
	Tetraodont 1											6.3	2	4.8(4.5-5)	Po	M
	Oceanic taxa															
Myctophidae	*Benthosema pterotum*		5.56				1	10							Po	F
	Total number of larvae		146	17	459	159	788		154	133	1503	268	2073			

Total number of larvae = 5569
Number of families = 41
Number of species = 63

The larvae of these estuarine independent taxa were in at least 16% of mainly mid-channel samples during day and night flood tides and night ebb tides (Table 10.4). The species *Thrysoidea macrura, H.quadrimaculatus* and Blenniid 1 were the most abundant estuarine-independent taxa and were mainly in night ebb mid-channel samples.

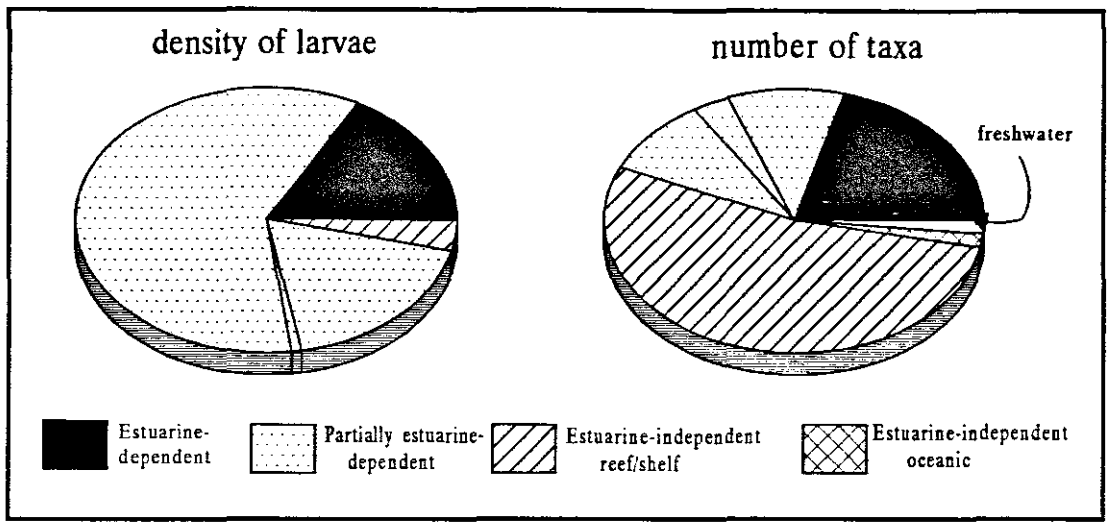


Figure 10.9. Percentage contribution of the estuarine-association categories, in terms of density of larvae and number of taxa, for all taxa sampled in both the February and March 24-h inlet studies

10.3.3.2 Temporal and Spatial Trends in Larval Abundance

Larval densities of all taxa together were significantly higher on flood tides ($P < 0.05$), at night time ($P < 0.01$) and at the edge site ($P < 0.001$) (Table 10.5). Larval densities of *C.mossambica,* in particular, were far greater on flood tides with a mean square of 4.33 ($P < 0.001$). Of the abundant species, only *S.holodon* had significantly higher densities on ebb tides ($P < 0.05$). The dominant taxa in each estuarine-association group had significantly higher densities at night, except Eleotrid 1, *M.cyprinoides* and *S.holodon* (Table 10.5). The higher densities of larvae at the edge site was particularly evident for the catadromous species *M.cyprinoides* ($P < 0.001$) and the partially estuarine-dependent species *C.chanos* ($P < 0.001$). The most significant 2-way interaction was the tide x site interaction for *S.holodon*, even though densities were not significantly different at the two sites.

Table 10.5. Mean squares and significance levels for three way ANOVAs of densities of the most abundant species in each estuarine-association group, in the nearshore coastal zone off the mouth of the St Lucia Estuary. (DF, degrees of freedom).

Estuarine-association group	Main effects			2-way interaction		
	Tide (F,E)[A] (DF=1)	Time (D,N))[B] (DF=1)	Site (ed,ch)[C] (DF=1)	Tide x Time (DF=1)	Tide x Site (DF=1)	Time x Site (DF=1)
All taxa	1.28*(F>E)	2.72**(N>D)	6.90***(ed>ch)	0.43	y	0.20
Estuarine-dependent	0.08	1.00	5.04***(ed>ch)	0.01	0.25	0.01
Electrid 1	0.32	0.31	0.38	<0.01	0.84*	0.03
Megalops cyprinoides	0.01	0.02	2.10***(ed>ch)	<0.01	0.21	0.46
Taenioides jacksoni	0.41(F>E)	0.60*(N>D)	0.13	0.29	0.08	0.09
Partially estuarine-dependent	0.90	3.83**(N>D)	5.32**(ed>ch)	1.55	0.59	0.09
Croilia mossambica	4.33***(F>E)	3.04**(N>D)	0.02	1.87*	0.01	0.20
Gobiid 1	1.17*(F>E)	2.90***(N>D)	0.24	0.06	0.02	1.01*
Chanos chanos	1.92**(F>E)	0.81*(N>D)	5.25***(ed>ch)	1.76**	1.11*	0.66
Stolephorus holodon	0.97*(E>F)	0.24	0.39	0.16	2.13***	0.79*
Estuarine-independent[D]						

*P < 0.05; **P < 0.01; ***P < 0.001

[A]tide where densities are significantly higher is indicated in parentheses. F, flood; E, ebb

[B]time where densities are significantly higher is indicated in parentheses. D, day; N, night

[C]site where densities are significantly higher is indicated in parentheses. ed, edge; ch, mid-channel

[D]not enough data for analysis

During the February 24-h sampling session densities of all taxa together ranged from 1.3 - 83 larvae per $100m^3$ (mean of replicate samples) with larvae being most abundant at the turn of the tide from night flood to day ebb, particularly at the edge site (Figure 10.10). Larval densities of estuarine-dependent and partially estuarine-dependent taxa followed a similar trend with peaks of 51 and 38 larvae per $100m^3$, respectively, at the edge site. At the mid-channel site, larval densities were highest on the night flood tide (33 larvae per $100m^3$), particularly for partially estuarine dependent taxa (Figure 10.10).

During the March 24-h session, exceptionally high densities of larvae were recorded, most of which were at the edge site on the night flood tide (1347 larvae per $100m^3$, Figure 10.11). Conversely, mid-channel densities only reached 104 larvae per $100m^3$ during the same period. Partially estuarine-dependent taxa were particularly abundant accounting for the very high densities on the night flood tide.

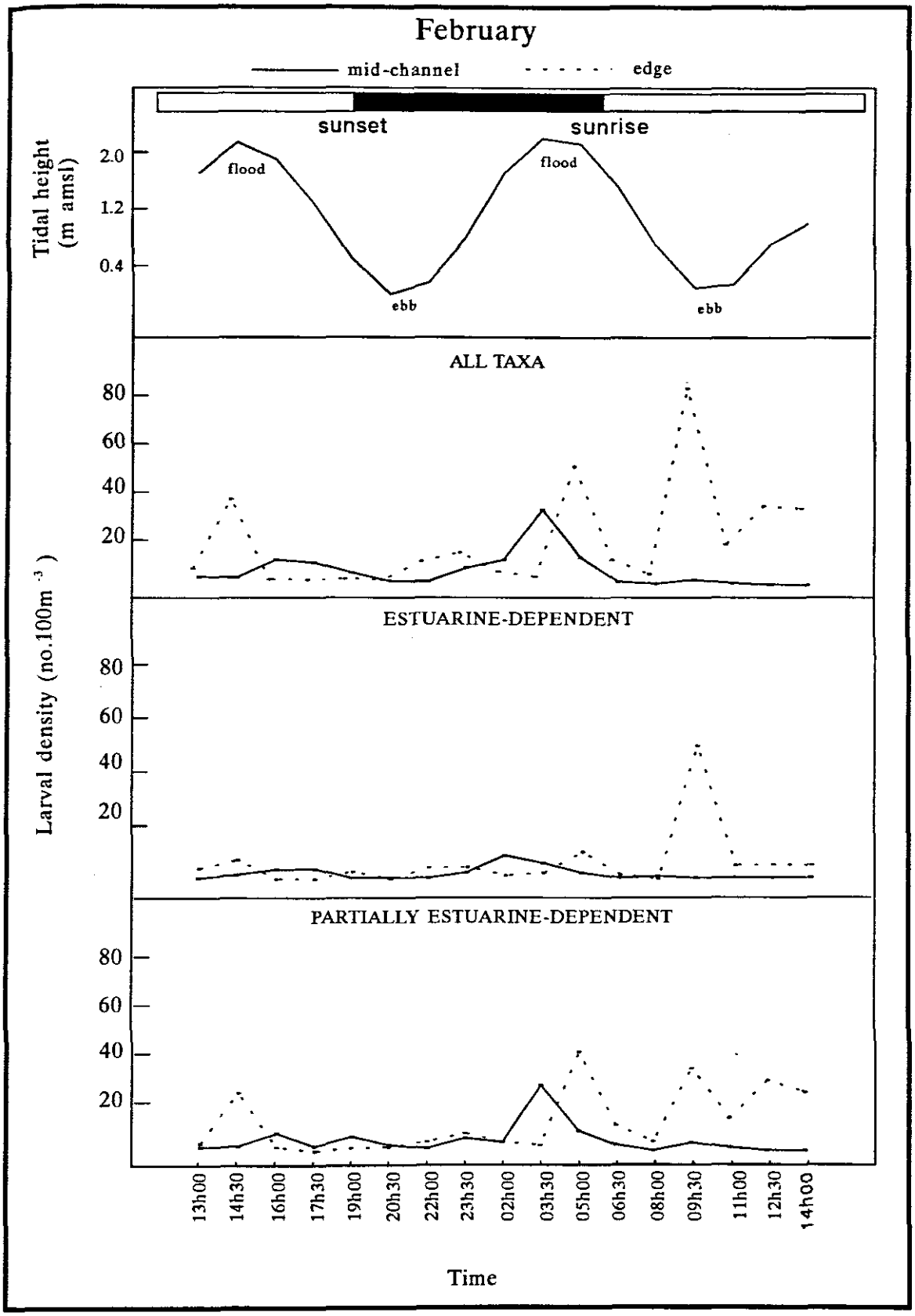


Figure 10.10. Changes in larval fish densities in the inlet of the St Lucia Estuary mouth, during the 24-h study in February 1994.

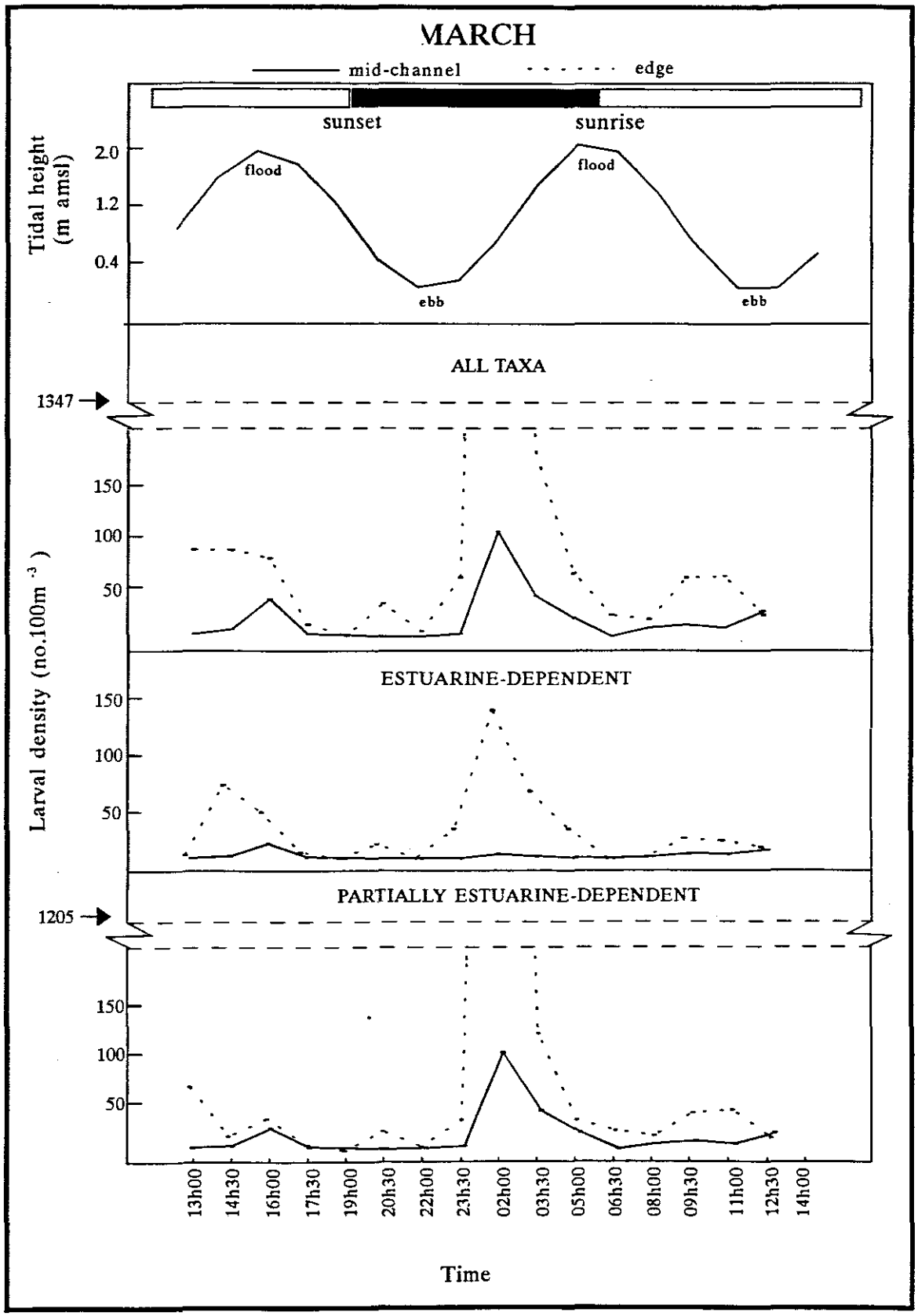


Figure 10.11. Changes in larval fish densities in the inlet of the St Lucia Estuary mouth, during the 24-h study in March 1994.

10.3.3.4 Developmental Stages

The mean size and range of all taxa (both February and March) for the mid-channel and edge site is given in Table 10.6. The larvae were predominantly postflexion with a few juveniles also being recorded. Leptocephalus larvae were the elopiformes, *M.cyprinoides* and *E.machnata,* and eel species.

Of the seven most abundant species, the mean size of only *C.mossambica* was significantly greater on flood tides compared to ebb tides ($F = 66.07$; $P < 0.0001$, Table 10.6). The mean sizes of three species differed significantly between day and night catches: *M.cyprinoides* and *S.holodon* had a greater mean size at night ($P < 0.001$); *C.mossambica* a greater mean size during the day ($P < 0.05$). The mean sizes of Eleotrid 1 and *C.chanos* were significantly greater in mid-channel samples ($P < 0.001$ and $P < 0.01$, respectively) whilst for *S.holodon* larvae were significantly larger in the edge samples ($P < 0.05$) (Table 10.6).

Larvae of the estuarine-dependent species Eleotrid 1 were most abundant in night ebb samples at the edge site and were all postflexion (Figure 10.12). *M.cyprinoides* larvae were also most abundant in edge samples during all four tide periods. No clear pattern is evident for *T.jacksoni* except most larvae were in edge samples on the night flood tide and all larvae were postflexion. For partially estuarine dependent taxa, three of the four dominant species, *C.mossambica,* Gobiid 1 and *C.chanos* were only collected as postflexion larvae and occurred predominantly during the night flood period at the edge site (Figure 10.13). The fourth dominant species, *S.holodon*, was present at all developmental stages with flexion and postflexion larvae being more abundant at the mid-channel site on flood tides, and as preflexion, flexion, postflexion and juvenile at the edge site on ebb tides.

Table 10.6. Mean body length (± 1SE) of abundant taxa collected in the two 24 h studies in the inlet at the St Lucia Estuary mouth. (3-way ANOVA's; F, F statistic).

Species	Main effects: Tide			Time			Site		
	Flood	Ebb	F	Day	Night	F	Channel	Edge	F
Estuarine-dependent									
Eleotrid 1	14.9 (0.09)	14.7 (0.08)	NS	14.8 (0.10)	14.8 (0.05)	NS	15.06 (0.09)	14.59 (0.08)	14.02***
Megalops cyprinoides	23.5 (0.33)	24.5 (0.48)	NS	22.9 (0.43)	25.1 (0.37)	17.87***	24.4 (0.50)	23.5 (0.30)	NS
Taenioides jacksoni	9.3 (0.05)	9.2 (0.07)	NS	9.2 (0.08)	9.2 (0.04)	NS	9.3 (0.06)	9.2 (0.06)	NS
Partially estuarine-dependent									
Croilia mossambica	11.0 (0.08)	9.2 (0.22)	66.07***	10.3 (0.17)	9.9 (0.11)	7.50*	10.1 (0.12)	10.1 (0.12)	NS
Gobiid 1	5.6 (0.05)	5.8 (0.08)	5.23*	5.7 (0.10)	5.8 (0.04)	NS	5.7 (0.06)	5.7 (0.07)	NS
Chanos chanos	11.7 (0.10)	11.7 (0.16)	NS	11.7 (0.13)	11.7 (0.12)	NS	12.0 (0.17)	11.4 (0.08)	11.12**
Stolephorus holodon	16.2 (1.07)	17.8 (0.87)	NS	12.5 (0.99)	21.4 (0.73)	48.86***	14.8 (0.96)	19.2 (1.02)0	7.68*

*p < 0.05; **p < 0.01; ***p < 0.001

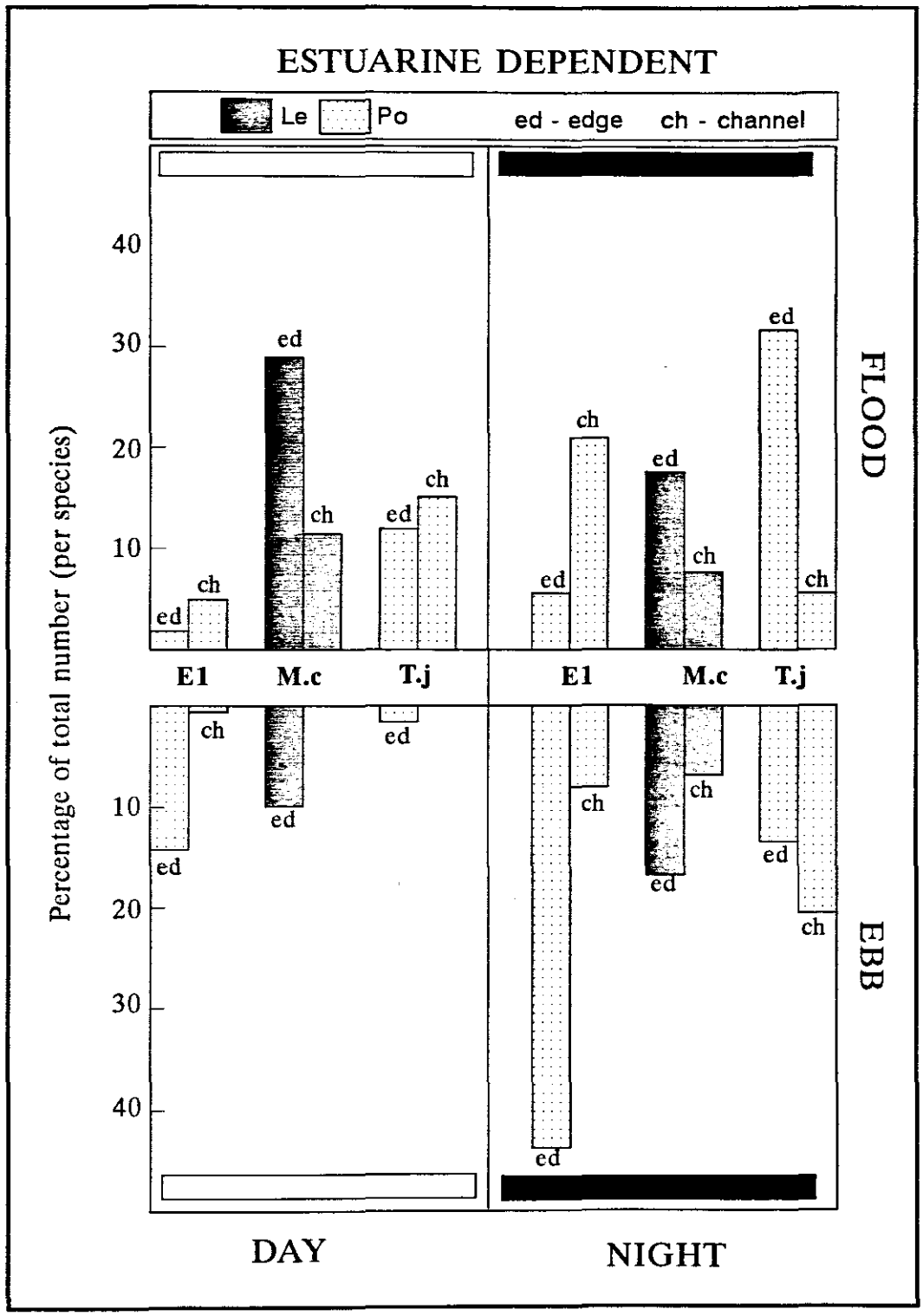


Figure 10.12. Percentage composition of developmental stages of larvae during each tidal period (Day Flood; Night Ebb; Night Flood; Day Ebb) of the dominant estuarine-dependent taxa (E1, Eleotrid 1; M.c, *M.cyprinoides*; T.j, *T.jacksoni*; Le, leptocephali; Po, postflexion).

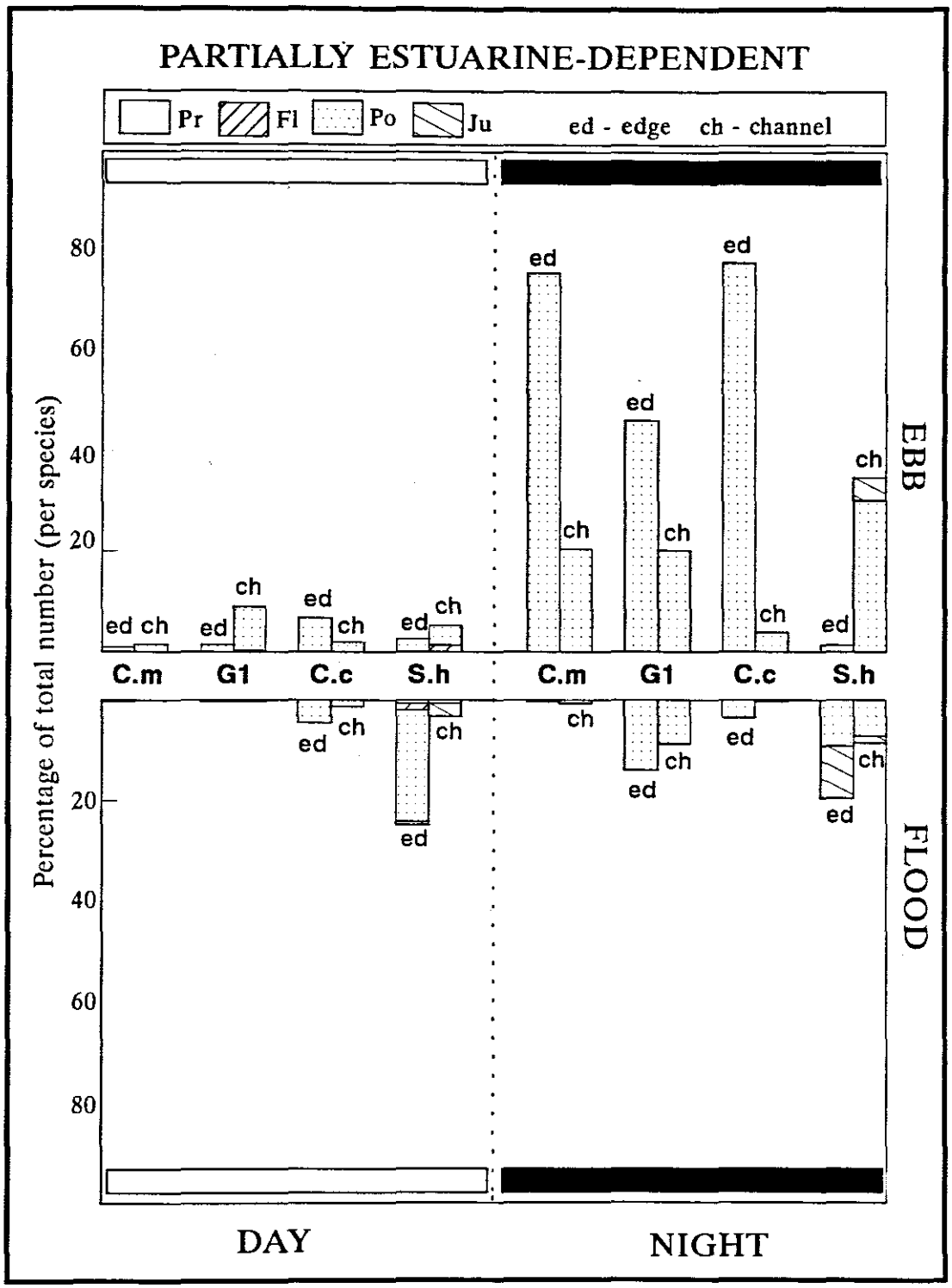


Figure 10.13. Percentage composition of developmental stages of larvae during each tidal period (Day Flood; Night Ebb; Night Flood; Day Ebb) of the dominant partially estuarine-dependent taxa (C.m, *C.mossambica*; G1, Gobiid 1; C.c, *C.chanos*; S.h, *S.holodon;* Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile)

10.4 Discussion

10.4.1 Structure of Larval fish Assemblages and Estuarine Dependence

The physical/environmental characteristics of a particular marine and estuarine habitat are important in structuring the fish community which resides there. Studies on juvenile and adult fish communities in Australia have shown that the type of nearshore habitat influences the species composition of the adjacent surf zone (Ayvazian and Hyndes 1995) and in adjacent estuaries (Blaber *et al.* 1995). These latter two studies recognised (from classification and ordination analysis) distinct assemblages within different zones which was related the physical characteristics of that habitat. This is also the case for larval fish stages, where well-defined assemblages of ichthyoplankton were found to occur in Conception Bay (Canada), and was related to variability in physico-chemical conditions of the water (Laprise and Pepin 1995). Classification and ordination of larval fish density data from the St Lucia region similarly showed the separation of larval fish communities into different assemblages was influenced by the environmental characteristics of each habitat.

An earlier study by Blaber *et al.* (1989) identified fish species which were restricted to or common to one or more of the different habitats sampled (Embley Estuary and Albatross Bay in northern Australia). They found that if a species was restricted to a habitat, such as the estuarine site, it was truly estuarine-dependent. Of the 47 abundant species used in the multivariate analysis of the present Chapter, nine species were restricted to the St Lucia Estuary, nine species restricted to the surf zone and seven species were common to both the estuary and surf zone (Table 10.2). This suggests that the nursery function of each of the three different habitats in the St Lucia region is species-specific.

10.4.2. Relationship of Environmental Factors to Assemblage Structure

Why are the larval fish communities in the estuary, surf zone and nearshore marine environment so distinct from one another ? This is related to the physical and environmental characteristics of each habitat. Water turbidity, alone and in combination with salinity and temperature, was the most important factor structuring the larval fish assemblages in Durban Harbour, Richards Bay Harbour and the St Lucia Estuary (see

Chapter 7). This was also the case in the present analysis although the correlations were weaker (Figure 7.7, Chapter 7; Figure 10.5). The relative importance of each of the environmental variables (turbidity, salinity and temperature) in influencing larval densities in the present study, and how this relates to findings of other workers is discussed in detail in section 4.3.2 (Chapter 4), section 5.3.2 (Chapter 5) and section 6.3.2 (Chapter 6) and so will not be discussed here. Essentially, other workers have found that water turbidity and/or salinity may be important cues for recruiting estuarine-associated fish larvae since, larval and juvenile fish densities responded to changes in those environmental variables (e.g.Whitfield 1994c).

The degree to which each environmental variable is important in structuring the assemblages of larvae depends upon the characteristics of that environment. Interannual and seasonal differences in species composition and abundance of fish larvae have been shown to be associated with differences in environmental conditions (Chiu and Hsyu 1994; Laprise and Pepin 1995). In the present study, each habitat was sampled in a different year hence somewhat different conditions prevailed (Table 10.1). Despite this interannual variability, each habitat has its own particular set of conditions which influences the structure of the larval fish community.

10.4.3. Mechanisms of Retention in the Estuarine Habitat

The mechanisms by which estuarine-associated fish species spawn offshore and subsequently move inshore to locate estuarine nursery sites is related to, but distinct from, retention in estuaries (Boehlert and Mundy 1988). Tidal currents are important in influencing the movement of fish larvae into and out of estuaries and is a combination of passive and active behavioural patterns of the larvae (Boehlert and Mundy 1988; Miller 1988). Beckley (1985) recorded catches of estuarine-associated species along the banks of the Swartkops Estuary mouth during ebb tides (Eastern Cape) and suggested that these species actively migrate towards the banks to avoid being back swept out to sea. A subsequent study by Whitfield (1989c), in the mouth of the Swartvlei Estuary (Western Cape), also indicated this mechanism of retention within the estuarine system. A more recent study by Raynie and Shaw (1994) examined the larval fish recruitment in Oyster Bayou tidal pass and results showed that during ebb tides, larger bay anchovy (*Anchoa*

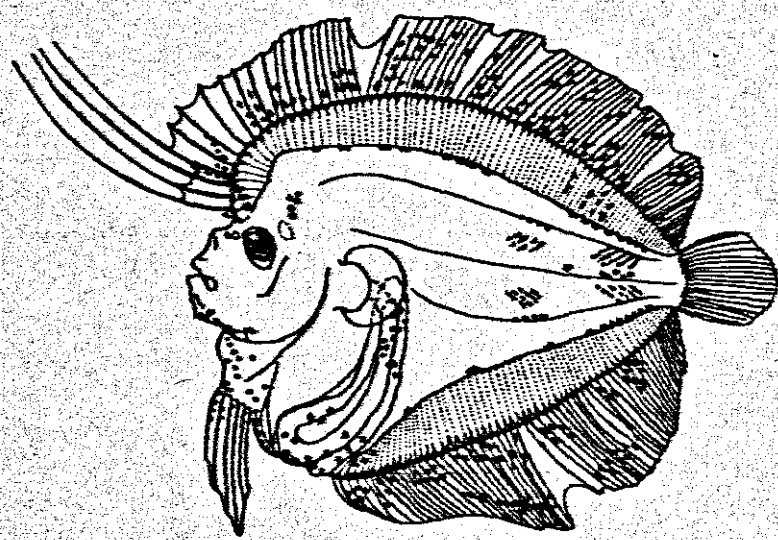
mitchilli) were particularly abundant along the pass edges. This suggested behaviourally mediated transport into and/or retention within Fourleague Bay (Louisiana). The majority of the fish larvae, in the present inlet study, were estuarine-associated species (95%) and were collected predominantly in edge samples (where current velocities are reduced - see Figure 2.5, Chapter 5) and on night flood tides. This implies a net influx of larvae into the estuarine environment. Larvae and early juveniles of estuarine-associated fish species entering the St Lucia estuarine system are, therefore, employing a mechanism of retention to avoid being washed back out to sea. However, additional inlet studies are needed to substantiate this finding.

A far greater number of larvae were sampled in the March 1993 session than in the previous month suggesting that this is a main recruitment period for fish larvae in the St Lucia region, although further research is required. Holt and Holt (1995) found that it is difficult to characterise a continuous process such as larval recruitment based on "snapshot" sampling., since, they found that the composition and abundance of fish larvae recruiting into Aransas Pass (Texas) varied substantially on an hourly and daily basis. This emphasises the need to do 24-h inlet studies on a seasonal and daily basis (for certain relevant periods) to get an overall picture of recruitment strategies of estuarine fish species. Simultaneous sampling in the offshore/nearshore zone and in the inlet of St Lucia Estuary would provide interesting results which would further our understanding of the ocean-estuarine coupling in the St Lucia Estuary.

In general, 24-h studies in the inlets of estuaries have recorded a prevalence of postflexion larvae and early juveniles of estuarine-associated species (Beckley 1985; Whitfield 1989c; Drake and Arias 1991; Neira and Potter 1992). The predominance of postflexion larvae and early juveniles of estuarine-associated species, in the present study; indicates that these species are capable of actively migrating into the St Lucia Estuary and are able to avoid being swept back out to sea by moving to the edges on ebb tides. Larvae of the marine stragglers were present on both flood and ebb tides at a range of developmental stages (Table 10.4) which suggests they are not being retained in the system. In contrast, Neira and Potter (1992) found that larvae of all the marine straggler species entered the Wilson Inlet only on flood and mainly at the preflexion stage. These larvae, therefore, presumably do not survive once in the estuarine habitat.

CHAPTER 11

Summary and Conclusions



11. SUMMARY AND CONCLUSIONS

11.1 Biogeographic Considerations

In all the estuarine and coastal systems sampled in the present study, Indo-Pacific species predominated the larval fish assemblages (see Appendix I). This suggests close affinities to the fish assemblages elsewhere in the Indo-Pacific region. Blaber (1981) suggested that it is necessary to examine the distribution of southern African ichthyofauna in relation to the marine ichthyofauna of the Indo-Pacific as a whole, in order to understand more fully the relationship of these fishes with the estuarine environment. The latter study found that the water conditions in many of the bays/estuaries in south-east Africa, Queensland and Western Australia, and south-east Asia were very similar to the estuaries in southern Africa i.e. high turbidity, fluctuating salinities and calm conditions. Hence, similar conditions attract similar fish species. In addition, the circulation of oceanic currents in the Indo-Pacific facilitates the dispersal of tropical forms in a southerly direction towards southern Africa (Heydorn 1978). The dominance of subtropical estuaries by species with tropical zoogeographic affinities is illustrated by the fact that more than 100 fish species associated with subtropical estuaries in southern Africa have distributions which extend into the tropics (Whitfield 1994b).

The larval fish assemblage in the nearshore coastal zone off St Lucia is particularly indicative of the close affinities to other regions in the Indo-Pacific (e.g. East China Sea and the Andaman Sea), with larval fish assemblages being very similar in terms of total numbers of larvae, number of taxa and number of families. Contributing to these similarities are the ecological requirements of larval fishes which must be adequate for the different species to establish themselves in a particular habitat. It would be useful to make a comparison of the larval fish communities in other subtropical estuaries in the southern hemisphere, such as Australia, to gain insight into the ecological requirements of larval fish occurring in estuarine environments in the region as a whole. However, the larval fish studies undertaken in Australia have been done in temperate estuaries (e.g. Gaughan *et al.* 1990; Neira and Potter 1994). A comparison of these studies with those in temperate estuaries in southern Africa (e.g. Beckley 1985;

Melville-Smith and Baird 1980) shows that there are some similarities and some dissimilarities in species composition which, in part, can be attributed to the different environmental conditions in the different estuaries. This emphasises the need for suitable environmental conditions for fish populations to be able to establish themselves in that particular environment. A case in point is the larval fish study at the small reef in the mouth of the Kosi Estuary (Harris *et al.* 1996). The lower part of this estuary has both estuarine and coral atoll lagoon characteristics which is reflected in the composition of the larval fish assemblage occurring there.

11.2 Community Structure

Results of the present study have shown that the assemblages of fish larvae occurring in the three large estuarine systems and adjacent nearshore zones in KwaZulu-Natal are diverse and form complex and dynamic communities. The structure of these assemblages depends upon a combination of factors, with changes in environmental conditions being one of the most important. Of the three environmental variables measured (salinity, temperature and turbidity) water turbidity was found to the most significant. Turbidity as a factor influencing distribution and abundance of fishes has also shown to be significant for juvenile and adult life history stages (Blaber 1981, 1987; Cyrus and Blaber 1987a,b; Marais 1988; Whitfield 1994c). This seems to be particularly relevant for subtropical southeast African estuaries (Blaber 1981), many of which are turbid environments. However, it is difficult to assess the relative importance of all the different environmental variables which may be influencing larval (and juvenile/adult) fish abundance and distribution since different researchers measured different variables and, sometimes, used different methods. Nevertheless, the present study has shown that the variables which were measured are all contributing significantly to changes in the larval fish densities and subsequently the assemblage structure.

The structure (size and mouth condition) of an estuarine habitat is also important in determining the community structure of the larval fish occurring in these habitats. This was clearly shown by the comparison of the larval fish assemblages in the St Lucia Estuary and the two harbours, Durban and Richards Bay (see Figure 7.9, Chapter 7). The condition of the mouth, and therefore amount of water exchange, determines the

extent to which marine species can penetrate the system and therefore dominate the larval assemblage. This is illustrated in the larval fish study in the Wilson Inlet, Western Australia, where the paucity of marine-spawned larvae within the estuary was attributed to the restricted tidal exchange at the mouth (Neira and Potter 1992). Larval fish assemblages near Indo-Pacific coral reefs are similarly strongly determined by habitat type and topography (Leis 1993).

In the nearshore coastal zones on the coast of New South Wales (Australia) and the East China Sea (south-east Asia) the composition of the larval fish assemblages are influenced primarily by the local current regimes and water masses in the region (Miskiewicz 1987; Gray 1993; Chiu and Hsyu 1994). This was also the case in the present study where the presence of larvae of certain fish species, such as myctophids and scrombrids, where indicative of the major influence of the Agulhas Current on the assemblage structure off St Lucia. Cowen *et al.* (1993) found that the structure of the larval fish assemblages within the Middle Atlantic Bight (U.S. eastern coast) was determined primarily by the physical processes that operate within the Bight. In the latter study, environmental variables such as salinity and temperature only accounted for < 15% of the variability in larval densities, which is similar to the present study in the St Lucia coastal waters (< 10% of the variation in larval densities - see Table 9.2, Chapter 9). This emphasises the need to have a good measure of the oceanographic features when studying larval fish assemblages in coastal habitats.

11.3 Estuarine-Dependence and Nursery Function

It is well established that estuarine environments function as nursery grounds for a number of marine fish species (e.g. Day *et al.* 1981; Haedrich 1983; Whitfield 1994a). In southern Africa 61 fish species have been recorded as being either completely or partially dependent on estuaries as nurseries and/or foraging areas, particularly as juveniles (Whitfield 1994a). This indicates that estuaries in South Africa are especially important as nursery sites, since there are few alternative sites which can function as nursery habitats (Potter *et al.* 1990). For both subtropical and temperate estuaries world-wide, a predominance of old larvae (postflexion) and early juveniles of marine fish species recruit into estuarine nursery areas from offshore (Day *et al.* 1981; Haedrich

1983; Claridge *et al.* 1986; Whitfield 1989a; Tzeng and Wang 1992; Cyrus and Forbes 1994; Neira and Potter 1994). The present study has further emphasised the importance of estuarine habitats as nursery sites for certain marine species at the postflexion larval stage, since a large proportion of the larvae of estuarine-associated fish species collected were old larvae. Alternative non-estuarine nursery habitats, such as surf zones and nearshore coastal areas, are also important nursery sites for certain marine fish species at the postflexion larval stage and juvenile stage (e.g. Modde 1980; Lenanton 1982; Bennett 1989b; Blaber *et al.* 1989; Whitfield 1989c). In South Africa, a number of marine fish species were found to be particularly abundant as old larvae in the surf zones of the Eastern Cape and KwaZulu-Natal (Whitfield 1989c; see Chapter 8 of present study). This suggests that the surf zone is playing a nursery function role on the coast of South Africa.

Human interference, such as bad farming techniques in river catchments and developments such as harbours, do impact on an estuarine system in one way or another. Hay *et al.* (1995), in their analysis of the biological status of shipping ports in KwaZulu-Natal, concluded that despite the impact of harbour development, the ichthyofauna in the ports was still diverse and relatively stable. The development of these ports is, therefore, not necessarily a "bad" thing and is likened to a terrestrial game reserve where management has attenuated physical extremes (Hay *et al.* 1995). Heydorn (1978b) stated that "many east coast estuaries are silted up to such an extent, as a result of erosion in catchments, that our commercial harbours must take over the important role of nurseries for many marine fish and prawn species". The present study substantiates this (see Chapter 7) since multivariate analysis portrayed the St Lucia system as more "unstable" than the two harbours. This is because the St Lucia Estuary is a more "typical" estuarine habitat which is inherently variable and unstable but which is exacerbated by the high siltation rates caused by bad catchment management. The statement above by Heydorn (1978b) is, therefore, significant in that Durban and Richards Bay Harbour are playing an important role in the life cycles of estuarine-associated fish species. KwaZulu-Natal harbours are also nursery grounds for a number of other marine organisms (penaeid prawns and portunid crab) further emphasising the need for a management policy for each harbour (Cyrus and Forbes 1996).

11.4 Recruitment Mechanisms

The present study has indicated that the recruitment process is a combination of both passive and active processes and links the offshore spawning grounds and inshore nursery habitats of the estuarine-associated fish species. Larvae reaching a particular developmental stage, and receiving an appropriate cue, actively seek suitable nursery habitats. Environmental factors together with ontogenetic behavioural responses and local current eddies results in a net shoreward movement of larvae to inshore nursery habitats. The origin of many of the larvae in the assemblages off the coast of St Lucia is probably from both local spawning populations in the shelf waters off KwaZulu-Natal and spawning populations further north in shelf waters off Mozambique. The 24-h surf zone study, in particular, demonstrated the response of recruiting fish larvae to the estuarine nursery habitat: unusually high numbers of estuarine-associated fish larvae were collected at the sand bar blocking the estuary mouth. This suggested that olfactory cues must be playing a part in the recruitment response of fish larvae.

But what are the actual mechanisms of this recruitment process ?. To further our understanding of the recruitment mechanisms of fish species, that use coastal systems as nurseries, a knowledge of the dynamics of the physical variables as well as the responses of the fish to these variables is needed (Miller 1988). Selective tidal stream transport as a mechanism of recruitment and retention in estuarine nursery areas is well established in the literature (e.g. Miller 1988), and is species-specific (Boehlert and Mundy 1988). To examine whether selective tidal stream transport is a mechanism utilised by fish larvae entering estuarine nurseries both flood and ebb tide samples need to be taken. In the present study, the two harbour systems and the 24-h inlet studies in the mouth of the St Lucia Estuary, examined both flood and ebb tides. These studies demonstrated that selective tidal stream transport is a mechanism utilised by certain species but that different mechanisms prevailed depending on the depth of the entrance channel. In both the deep and the shallow entrance channels i.e. the harbours and the St Lucia Estuary, respectively, recruiting fish larvae were most abundant on flood tides indicating a net input of larvae into the system. A difference in the retention mechanism was, however, detected between the deep and shallow entrance channels: in the harbour channels larvae were avoiding the outgoing ebb currents by migrating to mid- and bottom waters, whilst

in the St Lucia Estuary channel the larvae were migrating to the edge of the channel to avoid the outgoing ebb currents. The two local 24-h inlet studies undertaken in the Swartkops Estuary mouth (Beckley 1985) and the Swartvlei Estuary mouth (Whitfield 1989c) - both of which have shallow entrance channels - initially suggested that this mechanism of retention existed. The present study has thus provided further evidence of this mechanism, for certain estuarine-associated fish species.

The utilisation of recruitment and retention mechanisms by fish larvae entering KwaZulu-Natal estuaries and harbours has some implications. For those taxa where selective tidal stream transport was particularly evident (e.g. sciaenids), retention of these species in the estuarine system would occur to a greater extent than other species that do not have retention mechanisms. In other words, by determining which species are actively utilising tidal currents to enter and remain in an estuary and/or harbour it gives an indication of which species are utilising a system to a greater of lesser extent.

11.5 Research Methodology

Graphical, distributional, univariate and multivariate analyses all provide different angles of interpretation. In the present study, all these techniques were applied to the larval fish density data and all gave important information. The XY-graphs demonstrated seasonality patterns for both abiotic and biotic variables, whilst proportional graphics (pie diagrams and bar graphs) gave a simple measure of the dominance of different factors. Summary tables listing which species were collected in the study and details such as overall rank, total mean catch, body length and developmental stages provided important information to the reader which cannot be portrayed in graphics. The simple statistical techniques used, ANOVAs and stepwise regressions, provided a measure of the significance of certain patterns in spatial and temporal distributions. The univariate measures, species diversity and evenness indices, provided a simple measure of community structure but will not detect underlying patterns in community structure. The classification and ordination analysis was far more sensitive in detecting differences in community structure and gave important information on how and why the larval assemblages are structured the way they are. In summary, all the methods used have provided important and relevant information and should all be

applied in ecological studies such as the present one. In addition, by using different approaches to analyse ecological data certain patterns emerge which would otherwise have gone unnoticed. For example, the partial dominance curve (see Figure 7.2, Chapter2) shows that with the removal of the most dominant species the intermediate species are important in structuring the community, whilst, the cumulative curve does not show this.

11.6 Recommendations for Further Research

The original aims of the thesis (see Chapter 1) were all achieved to varying degrees and have been discussed in the relevant Chapters. Certain new questions arose from the analyses, however, which emphasised the need for further research in order to clarify some of the aims and to gain more insight into the controlling factors influencing larval fish abundance patterns and recruitment mechanisms.

From basic ecological work (like the present study) one can identify which species are significant in terms of overall abundance and whether larvae of commercially and recreationally important species are occurring in particular nursery habitats. This provides a basis and gives direction for further research studies aiming to gain insight into recruitment patterns and mechanisms of certain, important species.

The following is a list of recommendations for further research in recruitment studies of fishes in estuarine and coastal systems in KwaZulu-Natal, but which also applies to other regions in southern Africa:

- Identify larvae of certain important recreational and commercial fish species in the region and target the study at those species. Many studies elsewhere have examined the early life history stages of specific species, such as black sea bass (*Centropristis striata*), which are an important component of commercial fisheries.
- Examine seasonality patterns over long time periods i.e. at least four to five years, so that interannual patterns in abundances can be identified.
- Use an otolith microstructure-based technique which can determine the origin of recruiting fish larvae into inshore nursery areas.

- A recent study on benthic communities in a small KwaZulu-Natal estuary (the Siyaya Estuary) demonstrated the importance of measuring the physico-chemical characteristics (such as pH, oxygen, conductivity, chlorides) of the water since these variables influenced the abundances of the estuarine benthic fauna[1]. Since larval stages of fish are particularly sensitive to environmental change, these parameters should also be measured in future studies
- Simultaneous twenty-four hour studies in the inlets of estuarine systems and the adjacent nearshore marine environment would further our understanding in the recruitment process.
- One of the most important physical variables affecting larval fish distributions is the local current regime. Future studies, particularly in the nearshore coastal zone, should have adequate measurements of the oceanography and current systems in the study area.

In conclusion, it is clear that the estuarine and coastal systems in KwaZulu-Natal are valuable nursery sites for a number of marine fish species at the larval stage (predominantly postflexion) of their life cycle. The comparison of the three large estuarine systems indicated that different estuarine systems are utilised by different species and in varying degrees. Therefore, one cannot extrapolate from one system to another. For management decisions to be made regarding conservation of an estuarine nursery habitat, detailed studies are needed specifically for that habitat. The study on horizontal trends in larval fish abundance was important in identifying where certain species occur along the ocean-estuarine corridor and under what environmental conditions. This gave insight into which species are restricted to certain habitats and, therefore, their dependence on that habitat as a nursery site. This study has provided a firm basis for future research on recruitment of fish into estuarine systems along the KwaZulu-Natal coast. With the above mentioned "recommendations for future research" kept in mind, together with the results of the present study, one will gain invaluable information which will help manage and conserve the fish populations on our coastline.

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APPENDICES

APPENDICES

APPENDIX I

APPENDIX I: List of all taxa collected for all study sites ([A]Indo-Pacific, IP, distribution after Smith and Heemstra 19 [B]estuarine-association category after Whitfield 1994a)

FAMILY	SPECIES	DISTR[A]	CATEGORY[B]	DURBAN	RICHARDS BAY	ST LUCIA				KOSI
						ESTUARY	SURF	INLET	NEAR-SHORE	
Elopidae	*Elops machnata*	IP	IIa			+	+	+		
Megalopidae	*Megalops cyprinoides*	IP	Vb			+	+	+		
Anguillidae	*Anguilla mossambica*	IP	Va		+	+				+
Muraenidae	*Thyrsoidea macrura*	IP	IIIa		+	+		+		
	Muraenid 1		IIIa		+	+		+		
	Muraenid 2		IIIa							
Opichthidae	*Bascanichthys kirkii*	IP	IIIa			+				
	Opichthus sp.1	IP	IIIa		+	+		+		
	Opichthus sp.2	IP	IIIa	+	+				+	
	Opichthys sp.3	IP	IIIa		+				+	
	Opisurus serpens	IP	IIIa		+		+			
	Opichthid 1		IIIa	+	+	+		+		+
	Opichthid 2 (*Pseudmyrophis* ?)		IIIa						+	
	Opichthid 3		IIIa							
	Opichthid 4		IIIa	+						
Muraenisocidae	*Muraenasax bagio*	IP	IIIa		+	+		+		
Nettastomatidae	Nettastomid 1		IIIa						+	
Derichthyidae	*Nessorhamphus* sp.	IP	IIIa		+				+	+
Clupeidae	*Etrumeus teres*	IP	IIIa		+				+	
	Gichristella aestuaria		Ia		+	+			+	
	Herklotsichthys quadrimaculatus	IP	IIIa		+	+		+	+	+
	Hilsa kelee	IP	IIc			+				
	Pellona ditchela	IP	IIIa		+					
	Spratelloides delicatulus	IP	IIIa				+			
	Clupeid 1		IIIa						+	
	Clupeid 2		IIIa		+					
Engraulidae	*Stolephorus holodon*	IP	IIc	+	+	+	+	+	+	+
	Thryssa vitrirostris	IP	IIa			+	+	+		
	Thryssa setirostris	IP	IIIa			+	+	+		
Chirocentridae	*Chirocentrus dorab*	IP	IIIa				+			
Gonorhynchidae	*Gonorhynchus gonorhynchus*	IP	IIIa						+	+
Chanidae	*Chanos chanos*	IP	IIc							
Bathylagidae	*Bathylagus bericoides*	IP	IIIb	+						+
Stomiidae	*Stomias* sp.	IP	IIIb						+	
Chauliodontidae	*Chauliodus* sp.	IP	IIIb	+					+	
Astronesthidae	*Astronesthes* sp.	IP	IIIb						+	
Melanostomiidae	*Photonectes parvimanus*	IP	IIIb						+	
	Melanostomiid 1		IIIb	+					+	+
Photichthyidae	*Vinciguerria attenuata*	IP	IIIb				+		+	+
	Pollichthys mauli	IP	IIIb	+					+	
Gonostomatidae	*Diplophos taenia*	IP	IIIb						+	
	Cyclothone pseudopallida	IP	IIIb				+		+	+
	Gonostoma atlanticum (sp.1)	IP	IIIb						+	
	Gonostoma elongatum (sp.2)	IP	IIIb						+	
Sternophichthyidae	Sternopichthyid		IIIb						+	
Notosudidae	*Scopelosaurus* sp	IP	IIIb						+	+
Synodontidae	*Trachinocephalus myops*	IP	IIIa	+					+	
Paralepididae	*Lestidium atlanticum*	IP	IIIb						+	+
	Paralepid 1		IIIb	+					+	
Gadidae	Gadid 1		IIIa						+	
Bregmacerotidae	*Bregmaceros atlanticus*	IP	IIIa						+	
	Bregmaceros nectabanus	IP	IIIa						+	
Ophidiidae	*Brotula multibarbata*	IP	IIIa						+	
	Ophidiid 1		IIIb						+	
	Ophidiid 2		IIIb							+
Carapidae	Carapid 1		IIIa						+	
	Carapid 2		IIIa						+	
Bythitidae	*Dinematichthys* sp.	IP	IIIb						+	+
Antennariidae	*Histrio histrio*	IP	IIIb	+				+	+	+
Ogocephalidae	Ogocephalid		IIIb						+	
Ceratiidae	Ceratiid 1		IIIb						+	
	Ceratiid 2		IIIb	+					+	+
Gobiesocidae	*Lepadichthys* (sp.1)	IP	IIIa	+		+	+		+	
	Lepadichthys coccinotaenia (sp.2)	IP	IIIa				+		+	+
	Gobiesocid 1		IIIa			+				
	Gobiesocid 2		IIIa						+	
	Gobiesocid 3		IIIa	+						
Atherinidae	*Atherinomorus lacunosus*	IP	Ib	+			+			
	Atherinid 1		IIIa						+	
Notocheiridae	*Iso natalensis*	IP	IIIa	+	+	+			+	
Belonidae	*Strongylura lieura*	IP	IIc			+	+			

Hemiramphidae	*Hemiramphus far*		IIc			+				
	Hyporhamphus affinis	IP	IIc	+			+		+	+
Exocoetidae	Exocoetid 1		IIIa				+			
	Exocoetid 2		IIIa						+	
	Exocoetid 3		IIIa		+					
Trachipteridae	Trachipterid 1		IIIb						+	
Melamphidae	*Melamphaes* sp.	IP	IIIb						+	
Zeidae	*Zeus* sp.	IP	IIIa				+			
Pegasidae	*Eurypegasus draconis*	IP	IIIa		+					
Fistulariidae	*Fistularia commersonii*	IP	IIIa						+	
Syngnathidae	*Syngnathus acus*		Ib				+		+	
	Hippichthys heptagonus	IP	Ib		+	+	+		+	+
	Hippocampus sp. *(coronatus?)*	IP	IIIa				+			+
	Microphis fluviatilis		IV				+			
	Syngnathid 1		IIIa?				+			+
	Syngnathid 2		IIIa?				+			
	Syngnathid 3		IIIa?							+
Scorpaenidae	*Apistus carinatus*	IP	IIIa						+	+
	Minous sp. 1		IIIa	+					+	+
	Scorpaenid 1(*Sebastapistes strongia*)	IP	IIIa			+				
	Scorpaenid 2		IIIa				+			
	Scorpaenid 3		IIIa				+			
	Scorpaenid 4		IIIa				+			
	Scorpaenid 5		IIIa						+	
	Scorpaenid 6		IIIa						+	
	Scorpaenid 7		IIIa						+	
	Scorpaenid 8		IIIa						+	
	Scorpaenid 9		IIIa		+					
	Scorpaenid 10		IIIa	+						
Tetrarogidae	*Coccotropsis gymnoderma*		IIIa		+					
Caracanthidae	*Caracanthus* sp.	IP	IIIa						+	
Platycephalidae	*Platycephalus indicus*	IP	IIc		+				+	
	Platycephalid 1		IIIa						+	
	Platycephalid 2		IIIa	+					+	+
	Platycephalid 3		IIIa						+	+
	Platycephalid 4		IIIa							+
Dactylopteridae	*Dactyloptena orientalis*	IP	IIIa						+	
Ambassidae	*Ambassis gymnocephalus*	IP	Ib			+				
	Ambassis sp.		Ib?	+	+	+	+	+	+	+
Serranidae	*Epinephalus* sp.	IP	IIIa			+			+	
	Cephalopholis sp.	IP	IIIa						+	
	Anthias sp.	IP	IIIa	+						
Pseudochromidae	Pseudochromid 1		IIIa						+	
	Pseudochromid 2		IIIa						+	
Teraponidae	*Terapon jarbua*	IP	IIa			+	+	+	+	
	Pelates quadrilineatus	IP	IIc						+	
Priacanthidae	Priacanthid 1		IIIa	+					+	
Apogonidae	*Rhabdamia gracilis*	IP	IIIa	+					+	+
	Pseudamia gelatinosa	IP	IIIa						+	+
	Apogon sp.1	IP	IIIa							+
	Apogon sp.2	IP	IIIa				+		+	+
	Apogon sp. 3	IP	IIIa						+	+
	Foa sp.	IP	IIIa						+	
	Apogonid 1		IIIa						+	+
	Apogonid 2		IIIa							+
	Apogonid 3		IIIa						+	
	Apogonid 4		IIIa						+	
	Apogonid 5		IIIa						+	
	Apogonid 6		IIIa						+	
	Apogonid 7		IIIa						+	
	Apogonid 8		IIIa						+	
	Apogonid 9		IIIa						+	
	Apogonid 10		IIIa						+	
	Apogonid 11		IIIa	+						
Scombropidae	*Scombrops boops*		IIIa						+	
Haemulidae	*Pomadasys commersonnii*	IP	IIa		+	+	+	+		+
	Pomadasys kakaan	IP	IIc			+			+	+
	Pomadasys olivaceum		IIIa	+			+			
	Plectorhinchus sp.1	IP	IIIa				+			
	Plectorhinchus sp.2	IP	IIIa				+			+
	Haemulid 1		IIIa						+	

Lutjanidae	*Lutjanus argentimaculatus*	IP	IIc	+			+	+	+	+
	Lutjanid 1		IIIa		+				+	
	Lutjanid 2		IIIa							+
	Lutjanid 3		IIIa	+						
	Lutjanid 4		IIIa		+					
	Lutjanid 5		IIIa						+	
Sparidae	*Rhabdosargus holubi* (sp.1)		IIa		+	+	+			
	Rhabdosargus sarba/thorpei (sp. 2)	IP	IIa	+	+		+		+	
	Diplodus sargus capensis		IIc				+			
	Acanthopagrus berda	IP	IIa		+		+			+
	Pagellus bellottii natalensis		IIIa	+					+	
	Sparid 1		IIb			+				
	Sparid 2		IIIa						+	
	Sparid 3		IIIa						+	
	Sparid 4		IIIa						+	
	Sparid 5		IIc	+	+					
	Sparid 6		IIc	+						
	Sparid 7		IIIa						+	
Lethrinidae	*Lethrinus* sp.	IP	IIIa							+
	Lethrinid 1		IIIa						+	
Nemipteridae	*Nemipterus* sp.	IP	IIIa		+		+		+	
Scorpididae	*Neoscorpis lithophilus*	IP	IIIa				+			
Monodactylidae	*Monodactylus argenteus*	IP	IIa			+	+	+	+	
Gerreidae	*Gerres* sp.1	IP	IIc			+	+		+	
	Gerres sp.2		IIc				+			
Mullidae	Mullid 1		IIIa						+	
	Mullid 2		IIIa	+					+	+
Sillaginidae	*Sillago sihama*	IP	IIc			+			+	
Sciaenidae	*Johnius dussumeiri*	IP	IIc			+				
	Argyrosomus sp.		IIb		+					
	Umbrina ronchus	IP	IIIa	+	+	+	+		+	
	Atrobucca nibe	IP	IIIa				+			
	Sciaenid 1		IIIa						+	
	Sciaenid 2		IIb		+					
Leiognathidae	*Leiognathus equula*	IP	IIc						+	
	Secutor insidiator	IP	IIIa						+	
Pomacanthidae	Pomacanthid 1		IIIa						+	
Chaetodontidae	Chaetodontid 1		IIIa						+	
Bramidae	*Brama* sp.	IP	IIIa						+	
	Bramid 1		IIIa						+	
Carangidae	*Carangoides* sp.	IP	IIIa						+	+
	Scomberoides sp.	IP	IIIa						+	
	Trachinotus baillonii (sp.1)	IP	IIIa				+		+	
	Trachinotus blochii (sp.2)	IP	IIIa				+		+	
	Elagatis bipinnulata	IP	IIIa						+	
	Seriolina nigrofaciatus	IP	IIIa						+	
	Decapterus sp.1	IP	IIIa						+	+
	Decapterus sp.2	IP	IIIa	+	+				+	+
	Caranx sexfaciatus	IP	IIIa	+			+		+	
	Carangid 1		IIIa				+		+	+
	Carangid 2		IIIa							
	Carangid 3		IIIa						+	
	Carangid 4		IIIa		+				+	
	Carangid 5		IIIa						+	
	Carangid 6		IIIa						+	
	Carangid 7		IIIa		+					
	Carangid 8		IIIa	+						
Coryphaenidae	*Coryphaena hippurus*	IP	IIIb						+	
Cirrhitidae	Cirrhitid 1		IIIa						+	
Cheilodactylidae	Cheilodactylid		IIIa	+			+			
Pempheridae	*Parapriacanthus* sp.	IP	IIIa						+	
	Pempheris sp.1	IP	IIIa	+	+	+	+	+	+	
	Pempheris sp.2	IP	IIIa	+					+	
	Pempherid 1		IIIa						+	
Pomacentridae	*Abudefduf* sp.	IP	IIIa				+		+	
	Pomacentrus sp.	IP	IIIa							
	Pomacentrid 1		IIIa							+
	Pomacentrid 2		IIIa							+
	Pomacentrid 3		IIIa							+
	Pomacentrid		IIIa	+						
Labridae	*Xyrichthys* sp.1	IP	IIIa						+	
	Xyrichthys sp.2	IP	IIIa		+				+	+
	Labrid 1		IIIa						+	
	Labrid 2		IIIa						+	
	Labrid 3		IIIa						+	
	Labrid 4		IIIa			+			+	
	Labrid 5		IIIa						+	

	Labrid 6		IIIa						+	
	Labrid 7		IIIa						+	
	Labrid 8		IIIa				+			
	Labrid 9		IIIa				+			
	Labrid 10		IIIa							+
	Labrid 11		IIIa							+
	Labrid 12		IIIa							+
	Labrid 13		IIIa							+
	Labrid 14		IIIa							+
	Labrid 15		IIIa	+						+
	Labrid 16		IIIa							+
	Labrid 17		IIIa							+
	Labrid 18		IIIa							+
	Labrid 19		IIIa		+					
	Labrid 20		IIIa		+					
	Labrid 21		IIIa	+						
Scaridae	*Scarus* sp.	IP	IIIa	+		+	+		+	+
	Scarid 1		IIIa						+	
	Scarid 2		IIIa						+	
	Scarid 3		IIIa						+	
	Scarid 4		IIIa							+
	Scarid 5		IIIa	+						
Mugilidae	Mugilid 1		IIa	+		+	+	+		+
	Mugilid 2		IIc	+					+	
	Mugilid 3		IIb	+	+					
Polynemidae	*Polydactylus plebius*	IP	IIIa				+		+	
Sphyraenidae	*Sphyraena jello*	IP	IIc			+			+	
	Sphyraena sp.1	IP	IIc						+	
	Sphyraena sp.2	IP	IIIa							+
	Sphyraena sp.3	IP	IIIa							+
Opistognathidae	Opistognathid		IIIa						+	
Cepolidae	*Acanthocepepola limbata*	IP	IIIa						+	
	Cepolidae		IIIa						+	
Chiasmodontidae	Chiasmodont		IIIa						+	
Champsodontidae	*Champsodon capensis*	IP	IIIb						+	
Uranoscopidae	Uranoscopid		IIIb						+	
Trichonotidae	*Trichonotus marleyi*		IIIa	+				+	+	+
Creedidae	*Apocreedia vanderhorstii*		IIIa				+		+	+
	Limnichthys nitidus	IP	IIIa	+					+	+
Percophidae	*Bemprops* sp.		IIIb						+	
Mugiloididae	*Parapercis* sp.	IP	IIIa						+	+
Blenniidae	*Omobranchus banditus*		IIIa			+				
	Omobranchus sp.*(woodi)*		Ia	+		+	+		+	
	Istiblennius sp.		IIIa				+			+
	Blenniid 1		IIIa			+	+		+	+
	Blenniid 2		IIIa			+	+		+	
	Blennid 3		IIIa						+	
	Blenniid 4		IIIa				+			
	Blennid 5		IIIa				+			
	Blenniid 6		IIIa		+		+		+	+
	Blennid 7		IIIa						+	+
	Blenniid 8		IIIa	+						
Tripterygiidae	*Enneapterygius clarkae*	IP	IIIa			+				
	Tripterygiid 1		IIIa						+	
	Tripterygiid 2		IIIa						+	+
	Tripterygiid 3		IIIa						+	
	Tripterygiid 4		IIIa						+	
Clinidae	*Pavoclinus* sp.		IIIa							+
	Clinid 1		IIIa				+			
	Clinid 2		IIIa							+
Ammodytidae	*Embolichthys mitsukurii*	IP	IIIa						+	
	Ammodytid 1		IIIa						+	+
Callionymidae	Callionymid 1(*Draculo celetus*)		IIIa	+	+				+	+
	Callionymid 2		IIIa						+	
Schindleriidae	*Schindleria praematura*	IP	IIIa							
	Schindleria pitschmanni	IP	IIIa							
Gobiidae	*Callogobius* sp.		IIIa			+				
	Croilia mossambica		Ib	+	+	+	+	+	+	+
	Glossogobius callidus		Ib			+				
	Oligolepis acutipennis	IP	Ia			+				
	Oxyurichthes opthalmonema	IP	IIIa			+				
	Psammogobius knysnaensis		Ia			+	+	+	+	
	Redigobius sp.		Ia			+				
	Silhouetta sibayi		IV			+				
	Taenioides esquivel		Ib			+	+	+		
	Taenioides jacksoni		Ia			+	+	+		
	Trypauchen microcephalus	IP	Ib			+				

	Corygalops william		IIIa				+			
	Gobiid 1		Ib?			+	+	+		
	Gobiid 2		*Ib?*			+				
	Gobiid 3		IIIa?			+				
	Gobiid 4		IIIa?			+			+	
	Gobiid 5=Gobiid 10		IIIa?		+	+	+	+	+	+
	Gobiid 6		IIIa?			+				
	Gobiid 7		IIIa?		+		+	+	+	
	Gobiid 8		IIIa?				+	+		
	Gobiid 9		IIIa?				+			
	Gobiid 11		IIIa?				+			+
	Gobiid 12		IIIa?		+				+	
	Gobiid 13		*IIIa?*	+	+			+		
	Gobiid 14		IIIa?					+		
	Gobiid 15		IIIa?		+				+	+
	Gobiid 16		IIIa?						+	
	Gobiid 17		IIIa?						+	
	Gobiid 18		IIIa?						+	
	Gobiid 19		IIIa?						+	
	Gobiid 20		IIIa?						+	
	Gobiid 21		IIIa?							+
	Gobiid 22		IIIa?							+
	Gobiid 23		IIIa?							+
	Gobiid 24		IIIa?							+
	Gobiid 25		IIIa?							+
	Gobiid 26		IIIa?							+
	Gobiid 27		IIIa?		+					
	Gobiid 28		IIIa?		+					
	Gobiid 29		IIIa?		+					
	Gobiid 30		IIIa?		+					
	Gobiid 31		IIIa?		+					
Eleotridae	*Eleotris fusca*	IP	Ia			+				
	Eleotrid 1		Ia?			+				
	Eleotrid 2		Ia?		+	+	+	+		
	Eleotrid 3		Ia?			+				+
	Eleotrid 4		Ia?		+		+			
Siganidae	*Siganus sutor*	IP	IIIa			+				
Gempylidae	*Gempylus serpens*	IP	IIIa						+	
	Gempylid 1		IIIa	+						
	Gempylid 2		IIIa						+	
Trichiuridae	*Trichiurus lepturus*	IP	IIIa						+	
Scombridae	*Scomberomorus commerson* (sp.1)	IP	IIIa						+	
	Scomberomorus plurilineatus (sp.2)	IP	IIIa						+	+
	Restralliger kanagurta	IP	IIIa						+	
	Auxis rochei	IP	IIIa							+
	Scombrid 1		IIIa			+				
	Scombrid 2		IIIa			+			+	
	Scombrid 3		IIIa						+	+
	Scombrid 4		IIIa						+	
	Scombrid 5		IIIa						+	
	Scombrid		IIIa		+					
Amarsipidae	*Amarsipus* sp.		IIIb						+	
Nomeidae	*Cubiceps* sp.	IP	IIIb				+		+	+
	Psenes sp.	IP	IIIb						+	+
	Nomeid 1		IIIb						+	
Bothidae	*Engyprosopon grandisquama*	IP	IIIa				+		+	+
	Pseudorhombus sp.	IP	IIIa						+	+
Pleuronectidae	*Samaris cristatus*	IP	IIIa						+	+
Cynoglossidae	*Cynoglossus* sp.1	IP	IIIa			+				+
	Cynoglossus sp.2	IP	IIIa						+	
	Cynoglossus sp.3		IIIa						+	
	Cynoglossid 1		*IIIa*						+	+
	Cynoglossid 2		IIIa						+	+
Soleidae	*Solea bleekeri*		IIb			+	+	+	+	
	Soleid 1		IIIa				+			
	Soleid 2		IIIa				+			
	Soleid 3		IIIa						+	
Monacanthidae	*Stephanolepis auratus*		IIIa				+		+	
	Monacanthid 1		IIIa						+	
	Monacanthid 2		IIIa							+
Ostraciidae	*Lactoria gibbosus?*	IP	IIIa						+	
Tetraodontidae	*Lagocephalus inermis*	IP	IIIa			+			+	
	Arothron immaculatus	IP	IIIa			+	+			
	Amblyrhynchotes honckenii	IP	IIIa	+					+	
	Tetraodont 1		IIIa				+		+	

Others(identified -Leis)										
Balistidae	Balistid 1		IIIa						+	
Chlorapthalmidae	Chlorapthalmid 1		IIIa						+	
Anthinae	*Anthias* sp.		IIIa							
Myctophidae	*Benthosema pterotum*		IIIb			+	+		+	+
(all species predom	*Benthosema fibulatum*		IIIb				+		+	+
IP and/or C)	*Benthosema suborbitale*		IIIb						+	+
	Benthosema sp.1		IIIb						+	+
	Ceratoscopelus sp.		IIIb						+	+
	Hygophum hygomii		IIIb			+			+	+
	Hygophum proximum		IIIb			+			+	+
	Diaphus dilatematus		IIIb				+			
	Diaphus sp.?		IIIb							+
	Diaphus sp.1-mod slender		IIIb						+	+
	Diaphus sp.2-mod deep		IIIb		+				+	+
	Diaphus sp.3-deep		IIIb						+	+
	Diogenichthys atlanticus		IIIb				+			
	Diogenichthys panurgus		IIIb				+			
	Lampanyctus alatus		IIIb			+				+
	Lampanyctus lepidolychnus		IIIb						+	+
	Lampanyctes B		IIIb	+			+		+	+
	Scopelopsis multipunctatus		IIIb		+	+			+	+
	Symbolophorus barnardi		IIIb							+
	Symbolophorus evermanni		IIIb						+	+
	Myctophum spinosum		IIIb				+			
	Myctophid 1		IIIb							
	Myctophid 2		IIIb							
	Myctophid 3		IIIb							
	Myctophid 4		IIIb							
	Myctophid 5		IIIb							
	Myctophid 6		IIIb							
	Myctophid 7		IIIb							
	Myctophid 8		IIIb							
	Myctophid 9		IIIb							
	Myctophid 10		IIIb							
	Myctophum sp.		IIIb						+	
	Diogenichthys panurgus		IIIb						+	
	Diaphus mollis		IIIb						+	
	Triphoturus nigrescens		IIIb		+				+	
	Diaphus brachycephalus		IIIb		+				+	
	Lampandena sp.		IIIb	+					+	
	Myctophid 11		IIIb						+	
	Myctophid 12		IIIb						+	
	Myctophid 13		IIIb						+	
	Myctophum selenops		IIIb						+	
	Myctophum nitidum		IIIb						+	
	Ceratoscopelus warmingii		IIIb	+					+	
	Notoscopelus resplenmdens		IIIb						+	
	Lampanyctus pusillus		IIIb						+	
	Lobianchia gemellari		IIIb						+	
	Myctophum asperum		IIIb						+	
	Lampanyctus D		IIIb						+	
	Lampanyctinae		IIIb						+	
	Myctophid 14		IIIb						+	
	Taanichthys minimus		IIIb						+	
Unidentified	Unident 1								+	
	Unident 2								+	
	Unident 3								+	
	Unident 4								+	
	Unident 5								+	
	Unident 6								+	
	Unident 7								+	

APPENDIX II

APPENDIX II: Table 4.1 cont. (Durban Harbour)

Le, leptocephali; Pr, preflexion; Fl, flexion; Ju, juvenile
F, flood tide; E, ebb tide - *abundant; **very abundant)

Species	Total catch			Body length (mm)		Developmental stages	Presence	Ju & Ad present[A]
	no.	(mean no.100m^{-3})	%	mean	range			
ESTUARINE-INDEPENDENT								
Reef and shore taxa								
Decapterus sp.2	25	0.13	0.3	3.6	2.0-5.0	Pr,Fl	F*,E	
Iso natalensis	22	0.10	0.3	9.2	4.5-15.0	Pr,Fl,Po	F*,E	
Pagellus bellottii natalensis	24	0.10	0.3	4.3	3.0-8.0	Pr,Fl,Po	F,E	
Pomadasys olivaceum	27	0.10	0.3	11.5	7.0-22.0	Po	F,E	+
Scombrid 4	16	0.10	0.3	3.6	2.5-5.0	Pr	F,E	
Platycephalid 1	13	0.07	0.2	5.1	2.8-9.0	Pr,Fl,Po	F,E	
Gobiid 28	16	0.06	0.2	5.2	3.0-7.0	Pr,Fl,Po	F,E	
Mullid 2	13	0.05	0.1	4.2	2.5-6.0	Pr,Fl,Po	F,E	
Engyprosopon grandisquama	10	0.05	0.1	8.7	5.0-17.0	Pr,Fl,Po	F,E	
Carangid 4	11	0.05	0.1	4.4	3.0-5.0	Pr,Fl,Po	F,E	
Gobiid 29	10	0.05	0.1	11	9.0-16.0	Po	F,E	
Apistes carinatus	8	0.04	0.1	5.1	3.5-8.0	Pr,Fl,Po	F,E	
Lutjanus argentimaculatus	9	0.04	0.1	4.6	3.5-6.5	Pr,Fl	F,E	+
Brama sp.	8	0.04	0.1	4.5	3.0-5.0	Pr	F	
Etrumeus teres	9	0.04	0.1	18.7	10.0-29.0	Pr,Fl,Po	F,E	
Minous sp. 1	9	0.04	0.1	4.2	2.5-6.5	Pr,Fl	F,E	
Trachinocephalus myops	8	0.03	0.1	8	4.0-20.0	Pr,Fl,Po	F,E	
Bothid 1	7	0.03	0.1	4.6	3.0-6.0	Pr,Fl		
Scorpaenid 10	7	0.03	0.1	3	2.5-4.0	Pr	F,E	
Trichiurus lepturus	6	0.03	0.1	7.1	5.0-9.0	Pr,Fl	F,E	+
Pempheris sp.2	6	0.03	0.1	2.9	2.0-4.0	Pr	F,E	
Cheilodactylid	6	0.03	0.1	4.3		Pr	F	
Bregmaceros nectabanus	4	0.02	0.1	3.1	2.5-4.0	Pr	F,E	
Pempheris sp. 1	6	0.02	0.1	4.6	3.0-5.0	Pr,Fl,Po	F,E	
Stephanolepis auratus	5	0.02	0.1	7.3	2.5-18.5	Pr, Po	F,E	
Pseudorhombus sp.	5	0.02	0.1	5.3	3.0-8.5	Pr,Fl	F,E	
Carangoides sp.	5	0.02	0.1	5.1	2.5-14.0	Pr,Po	F,E	
Rhabdamia gracilis	4	0.01	<0.1	7.7	5.4-12.0	Po	E	-
Gempylid 1	3	0.01	<0.1	4.8	3.5-6.0	Pr,Fl	F	
Caranx sexfaciatus	3	0.01	<0.1	12.8	4.5-29.0	Po,Ju	F,E	
Opichthys sp.2	3	0.01	<0.1	17	9.0-30.0	Le	F	
Apocreedia vanderhorstii	1	0.01	<0.1	14		Po	F	
Tripterygid 2	2	0.01	<0.1	4.8	4.5-5.0	Pr,Fl	F	
Apogonid 11	1	0.01	<0.1	4.8		Fl	E	
Scarus sp.	3	0.01	<0.1	8.5	8.0-9.5	Po	F,E	
Trichonotus marleyi	3	0.01	<0.1	17.3	12.0-22.0	Po	F,E	
Soleid 2	2	0.01	<0.1	3.5	3.0-4.0	Pr	F,E	
Cepolid 1	2	0.01	<0.1	3.7	3.0-4.3	Pr	F,E	
Diogramma pictum	2	0.01	<0.1	10		Po		
Carangid 8	2	0.01	<0.1	4		Pr,Fl	F,E	
Sphyraena sp.4	2	0.01	<0.1	3.8	3.5-4.0	Pr	F	
Gobiid 5	2	0.01	<0.1	9.5	7.0-12.0	Po	F,E	
Syngnathid 2	2	0.01	<0.1	18.5	14.0-23.0	Po	F,E	
Mene maculata	2	0.01	<0.1	6.5	5.0-8.0	Po	F,E	
Xyrichthys sp.2	2	0.01	<0.1	14		Po	E	
Hippocampus sp.	2	0.01	<0.1	9	8.5-9.5	Po	F	
Schindleria praematura	2	0.01	<0.1	13	11.0-15.0	Ju,Ad	F,E	
Histrio histrio	2	0.01	<0.1	3.9	3.8-4.0	Fl	F,E	
Opichthid 1	2	0.01	<0.1	96	94.0-98.0	Le	E	
Pellona ditchella	1	0.01	<0.1	10		Pr	F	
Blennid 8	1	0.01	<0.1	4.5		Pr	F	
Callogobius sp.	1	0.01	<0.1	5.5		Fl	F	
Labrid 3	1	0.01	<0.1	4		Po	F	
Carangid 5	1	0.01	<0.1	5		Pr	F	
Opichthid 4	1	0.01	<0.1	4		Le	F	

Chaetodontid 1	2	<0.01	<0.1	3.8	3.5-4.0	Pr	E	
Scombrid 3	1	<0.01	<0.1	7		Po	F	
Sphyraena sp. 3	1	<0.01	<0.1	5.5		Fl	F	
Sparid 5	1	<0.01	<0.1	8		Po	F	
Priacanthid 1	1	<0.01	<0.1	6		Pr	E	
Coryphaena hippurus	1	<0.01	<0.1	6.5		Pr	E	
Omobranchus banditus	1	<0.01	<0.1	5.5		Fl	F	
Limnichthys nitidus	1	<0.01	<0.1	12		Po	E	
Opichthid 3	1	<0.01	<0.1	4		Po	F	
Cirrhitid 1	1	<0.01	<0.1	7		Po	F	
Scomberoides sp.	1	<0.01	<0.1	4.5		Fl		
Anthias sp.	1	<0.01	<0.1	5.5		Po	E	+
Mullid 1	1	<0.01	<0.1	5		Fl	F	
Gempylid 2	1	<0.01	<0.1	22		Pr	F	
Muraenosox bagio	1	<0.01	<0.1	4.5		Le	E	
Bothid 2	1	<0.01	<0.1	3.5		Pr		+
Labrid 21	1	<0.01	<0.1	5		Po	F	
Gobiid 14	1	<0.01	<0.1	7		Po	E	
Labrid 19	1	<0.01	<0.1	10		Po	F	
Lutjanid 3	1	<0.01	<0.1	3.8		Pr	E	
Gobiesocid 3	1	<0.01	<0.1	4		Pr		
Oceanic taxa								
Lampandena sp.	14	0.06	0.2	6.1	3.5-9.0	Pr,Fl,Po	F*,E	
Melanostomid 1	13	0.05	0.1	19	7.0-32.0	Pr,Fl,Po,Ju	F*,E	
Lampanyctes B	11	0.05	0.1	3.6	3.0-5.0	Pr,Fl	F,E	
Triphoturus nigrescens	7	0.03	0.1	6.7	4.0-10.0	Pr, Po	F	
Ceratoscopelus warmingii	4	0.02	0.1	5.2	4.0-6.0	Pr,Fl,Po	F	
Scopelosaurus sp.	4	0.02	<0.1	13.3	12.0-16.0	Pr,Fl,Po	F	
Paralepid 1	3	0.02	<0.1	9.7	7.0-12.0	Pr	F	
Diogenichthys panurgus	2	0.01	<0.1	5	4.5-5.5	Pr	F,E	
Diaphus brachycephalus	2	0.01	<0.1	5.8	5.5-6.0	Po	F	
Pollichthys mauli	2	0.01	<0.1	24.5	23.0-26.0	Po	F	
Bathylagus bericoides	1	0.01	<0.1	6		Pr	F	
Ceratid 2	1	<0.01	<0.1	5		Pr,Fl,Po	F,E	
Astronesthes sp.	1	<0.01	<0.1	13		Fl	E	
Benthosema pterotum	1	<0.01	<0.1	5		Po	E	
Lestidium atlanticum	1	<0.01	<0.1	11		Po	F	
Psenes sp.	1	<0.01	<0.1	7		Po	F	
Chauliodus sp.	1	<0.01	<0.1	10		Pr	F	
Lobianchia gemellari	1	<0.01	<0.1	7		Po	F	
Champsodon capensis	3	<0.01	<0.1	4	2.0-6.0	Pr,Po	F,E	

[A]Wallace 1975a; Hay *et al.* (1993); Beckley *et al.* (1994); Guastella (1994)

APPENDIX III

APPENDIX III: Table 5.1 cont. (Richards Bay Harbour)

Gl, glass eel; Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile; Ad, adult; F, flood tide; E, ebb tide - *abundant; **very abundant

Species	Total catch			Body length (mm)		Developmental stage	Presence	Ju & Ad present^
	no	mean no.100m^{-3}	%	mean	range			
ESTUARINE-INDEPENDENT								
Reef and shore taxa								
Etrumeus teres	14	0.05	0.2	13.0	5.0-20.0	Pr,Fl,Po	F*,E	
Gobiid 31	9	0.04	0.1	8.2	6.0-12.0	Po	F	
Tripterygiid 1	7	0.03	0.1	4.9	3.0-6.0	Pr,Fl,Po	F,E	
Gobiid 29	5	0.02	0.1	11.7	7.5-23.0	Po,Ju	F,E	
Rastrelliger kanagurta	5	0.02	0.1	3.5	3.0-4.0	Pr	F	
Nemipterus sp.	5	0.02	0.1	3.0		Pr,Fl	F,E	
Brama sp.	4	0.02	0.1	4.5	3.5-6.0	Pr,Fl	F	
Scarus sp.	4	0.02	0.1	4.2	3.5-5.0	Pr	F,E	
Gobiid 5	4	0.01	0.1	8.4	7.0-10.0	Po	F,E	
Secutor insidiator	3	0.01	0.0	11.8	3.5-27.0	Fl,Po,Ju	F,E	
Cynoglossus sp.1	4	0.01	0.0	7.1	2.0-11.0	Pr,Po	F,E	
Arothron immaculatus	3	0.01	0.0	3.3	2.0-6.0	Pr,Po	F,E	+
Mullid 2	3	0.01	0.0	3.7	3.0-5.0	Pr,Po	F,E	
Clupeid 1	3	0.01	0.0	9.2	4.0-12.5	Pr,Fl	E	
Decapterus sp.2	2	0.01	0.0	3.8	3.5-4.0	Pr	F	
Carangid 4	2	0.01	0.0	5.9	4.8-7.0	Fl,Po	F	
Pseudorhombus sp.	2	0.01	0.0	9.8	9.0-10.5	Po	F	
Umbrina ronchus	2	0.01	0.0	6.5	6.0-7.0	Po	F	
Gobiid 30	2	0.01	0.0	3.5	3.0-4.0	Pr	F,E	
Labrid 19	2	0.01	0.0	6.5	4.0-9.0	Pr,Po	F	
Scombrid 6	2	0.01	0.0	3.5	3.0-4.0	Pr	F	
Nessorhamphus sp.	2	0.01	0.0	63.5	27.0-100.0	Le	F,E	
Gobiid 7	2	0.01	0.0	12.8	12.5-13.0	Po	F,E	
Bregmaceros atlanticus	2	0.01	0.0	19.8	9.5-30.0	Po	E	
Exocoetid 3	2	0.01	0.0	5.0		Po	F	
Ophisurus serpens	2	0.01	0.0	145.0	100.0-190.0	Le,Ju	F	
Amblyrhynchotes honckenii	2	0.01	0.0	2.3	2.0-2.5	Pr	F	+
Scombrops boops	2	0.01	0.0	12.4	11.8-13.0	Po	F	
Bascanichthys kirkii	1	0.01	0.0	64.0		Le	E	
Tylerius spinosissimus	2	0.00	0.0	5.0	4.0-6.0	Pr,Po	E	
Opichthus sp.2	1	0.00	0.0	10.0		Le	F	
Opichthid 1	1	0.00	0.0	113.0		Le	F	
Rhabdamia gracilis	1	0.00	0.0	5.0		Fl	E	
Muraenid 1	1	0.00	0.0	90.0		Le	E	
Iso natalensis	1	0.00	0.0	11.0		Po	E	
Lutjanid 4	1	0.00	0.0	3.0		Pr	F	
Pempheris sp.1	1	0.00	0.0	2.0		Pr	F	
Engyprosopon grandisquama	1	0.00	0.0	5.0		Pr	E	
Gobiid 15	1	0.00	0.0	7.0		Po	F	
Carangid 7	1	0.00	0.0	3.0		Pr	F	
Tripterygiid 4	1	0.00	0.0	6.0		Po	E	
Lutjanid 1	1	0.00	0.0	4.0		Pr	E	
Opichthus sp.1	1	0.00	0.0	80.0		Le	F	
Scombrid 1	1	0.00	0.0	4.0		Pr	E	
Eurypegasus draconis	1	0.00	0.0	7.5		Po	F	
Choeroichthys smithi	1	0.00	0.0	23.0		Po	F	
Coccotropsis gymnoderma	1	0.00	0.0	7.0		Po	F	
Muraenosox bagio	1	0.00	0.0	98.0		Le	E	+
Labrid 20	1	0.00	0.0	8.0		Po	E	
Nomeid 1	1	0.00	0.0	9.5		Po	E	
Mullid 1	1	0.00	0.0	4.9		Fl	F	
Thryssa setirostris	1	0.00	0.0	25.0		Po	E	
Eleotrid 4	1	0.00	0.0	12.0		Po	F	
Apistus carinatus	1	0.00	0.0	5.0		Po	E	
Thrysoidea macrura	1	0.00	0.0	68.0		Le	F	

Oceanic taxa								
Diaphus sp. 2	13	0.05	0.2	6.2	4.5-8.0	Pr,Fl,Po	F,E	
Scopelopsis multipunctatus	4	0.02	0.1	4.9	4.5-5.5	Pr,Fl	F,E	
Triphoturus nigrescens	4	0.01	0.0	4.8	4.0-6.0	Fl,Po	F,E	
Vinciguerria attenuata	2	0.01	0.0	10.3	8.0-12.5	Po	F,E	
Diaphus brachycephalus	1	0.00	0.0	6.0		Po	E	
Lestidium atlanticus	1	0.00	0.0	7.0		Pr	E	
Symbolophorus evermanni	1	0.00	0.0	5.2		Pr	E	
Hygophum hygomii	1	0.00	0.0	4.0		Pr	E	
Coryphaena hippurus	1	0.00	0.0	11.0		Po	F	
Champsodon capensis	1	0.00	0.0	4.0		Pr	F	
Myctophid 12	1	0.00	0.0	6.0		Po	F	

[A]Millard and Harrison (1954); van der Elst (1974-1986); Hay *et al.* (1993)

APPENDIX IV

APPENDIX IV: Table 8.1 cont. (Surf zone study, St Lucia)

Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile; Ad, adult; D, day; N, night - *abundant, **very abundant)

Species	Total catch			Body length (mm)		Developmental stage	Presence	Ju & Ad present [A]
	no	mean no.100m^{-3}	%	mean	range			
ESTUARINE-INDEPENDENT								
Reef and shore taxa								
Atrobucca nibe	4	0.05	0.1	13.5	8.0-24.0	Po	D,N	
Lepadichthys sp.1	4	0.05	0.1	5.3	4.8-6.0	Po	D	
Trachinotus sp.2	3	0.04	0.1	22.3	17.0-30.0	Po,Ju	N	
Soleid 2	3	0.04	0.1	4.2	3.5-4.5	Fl,Po	D	
Scarus sp.1	3	0.04	0.1	9.5	9.0-10.5	Po	D,N	+
Schindleria praematura	3	0.04	0.1	5.2	5.0-5.5	Po	D	
Ophisurus serpens	2	0.03	0.1	70.0		Le	N	
Atherinomorus lacunosus	2	0.02	0.1	18.5	18.0-19.0	Po	D	
Scorpaenid 3	2	0.02	0.1	3.5		Pr	D	
Etrumeus teres	1	0.02	<0.1	6.0		Pr	D	
Draculo celetus	1	0.02	<0.1	13.0		Po	N	
Blennid 5	1	0.02	<0.1	14.0		Po	N	
Exocoetid 1	1	0.02	<0.1	6.0		Po	D	
Scorpaenid 4	1	0.01	<0.1	4.0		Pr	N	
Clinid 1	1	0.01	<0.1	9.2		Po	N	
Strongylura leiura	1	0.01	<0.1	8.0		Po	N	+
Sparid 3	1	0.01	<0.1	7.0		Po	N	
Zeus sp.	1	0.01	<0.1	4.0		Pr	D	
Scorpaenid 2	1	0.01	<0.1	5.0		Fl	D	
Xyrichthys sp.1	1	0.01	<0.1	10.0		Po	N	
Trachinotus baillonii	1	0.01	<0.1	17.0		Po	D	
Omobranchus sp.	1	0.01	<0.1	5.0		Po	N	+?
Apogon sp.2	1	0.01	<0.1	5.0		Po	D	
Abudefduf sp.	1	0.01	<0.1	5.0		Po	D	
Apodocreedia vanderhorsti	1	0.01	<0.1	14.0		Po	N	
Choeroichthys smithi	1	0.01	<0.1	23.0		Po	N	
Plectorhinchus sp. 2	1	0.01	<0.1	19.5	15.0-24.0	Po	N	
Auxis rochei	1	0.01	<0.1	3.0		Pr	N	
Carangid 1	1	0.01	<0.1	2.5		Pr	D	
Blennid 1	1	0.01	<0.1	3.0		Pr	D	+
Corygalops william	1	0.01	<0.1	10.0		Po	D	
Hippocampus sp.	1	0.01	<0.1	7.0		Po	N	
Oceanic taxa								
Diaphus diadematus	4	0.05	0.1	3.4	3.2-3.8	Pr	D,N	
Myctophid 2	4	0.05	0.1	4.7	3.8-5.2	Pr	D	
Benthosema pterotum	4	0.04	0.1	4.7	3.2-7.0	Pr,Fl,Po	D	
Vinciguerria attenuata	4	0.04	0.1	9.5	9.0-10.0	Po	D	
Cubiceps sp.	3	0.03	0.1	4.3	3.2-5.0	Pr,Fl,Po	N	
Triphoturus nigrescens	2	0.03	0.1	3.2		Pr	N	
Cyclothone sp.	2	0.03	0.1	10.3		Po	D,N	
Lamparyctus sp.B	2	0.03	0.1	7.5	4.5-10.5	Pr,Po	D	
Diogenichthys atlanticus	2	0.02	0.1	4.7	4.4-4.9	Pr	D	
Benthosema fibulatum	1	0.01	<0.1	4.8		Fl	D	
Myctophum spinosum	1	0.01	<0.1	4.5		Pr	D	
Myctophid 1	1	0.01	<0.1	5.0		Pr	D	
Diogenichthys panurgus	1	0.01	<0.1	8.0		Po	D	

[A]Wallace (1975a,b); Wallace abd van der Elst (1975); Whitfield (1980)

APPENDIX V

APPENDIX V: Table 9.1 cont. (Nearshore coastal zone study, St Lucia)

Le, leptocephali; Pr, preflexion; Fl, flexion; Po, postflexion; Ju, juvenile;

Species	Total catch			Body length (mm)		Developmental stage
	no.	(mean no.100m^{-3})	%	Mean	Range	
ESTUARINE INDEPENDENT						
Marine stragglers						
Sphyraena sp.1	4	0.01	0.1	6.0	4.8-7.5	Pr,Fl,Po
Gobiid 7	2	0.01	0.1	13.1	13.0-13.2	Po
Callionymid 2	5	0.01	0.1	4.3	3.5-4.9	Pr,Po
Apocreedia vanderhorstii	3	0.01	0.1	8.5	8.5	Fl
Acanthocepola limbata	3	0.01	0.1	6.0	5.5-7.0	Pr
Decapterus sp.2	3	0.02	0.1	5.6	4.5-7.0	Po
Nessorhamphus sp.	4	0.02	0.1	13.1	5.0-22.0	Le
Cynoglossus sp.2	3	0.02	0.1	11.0	11.0	Po
Opistognathid	5	0.02	0.1	3.9	3.0-5.2	Fl
Ammodytid 1	3	0.02	0.1	3.8	3.0-4.5	Pr
Scombrid 4	5	0.02	0.1	3.2	2.5-4.0	Pr
Scomberomorus sp.1	5	0.02	0.1	6.4	3.8-8.8	Pr,Po
Carangoides sp.	3	0.02	0.1	4.7	4.0-5.0	Pr,Po
Sciaenid 1	3	0.02	0.1	7.7	6.0-9.0	Fl,Po
Sparid 4	4	0.02	0.1	6.8	6.0-8.0	Fl,Po
Polydactylus plebeius	3	0.02	0.1	2.6	2.5-2.9	Pr
Scorpaenid 7	4	0.02	0.1	5.0	2.5-7.0	Pr,Fl
Blenniid 1	4	0.02	0.1	6.8	4.0-8.0	Pr,Po
Trachinotus baillonii	4	0.02	0.1	14.3	8.0-17.0	Po
Brotula multibarbata	5	0.02	0.1	6.7	3.5-17.0	Pr,Po
Apogonid 1	6	0.03	0.1	4.6	4.0-5.5	Fl,Po
Scarus sp.	8	0.03	0.1	5.2	4.0-8.5	Pr,Fl,Po
Iso natalensis	7	0.03	0.1	6.6	2.5-11.0	Pr,Fl,Po
Parapercis sp.	7	0.03	0.1	5.0	4.0-7.0	Pr,Po
Sparid 7	6	0.03	0.1	7.8	6.5-9.0	Pr,Po
Carangid 3	3	0.03	0.1	4.2	3.5-5.0	Pr,Fl
Seriolina nigrofaciatus	8	0.03	0.1	4.0	3.0-5.9	Pr,Po
Pseudochromid 1	7	0.03	0.1	4.6	4.0-5.5	Pr,Fl
Scindleria praematura	8	0.03	0.1	5.0	3.0-8.0	Po
Pagellus bellottii natalensis	7	0.03	0.1	7.6	4.5-10.5	Fl,Po
Trichiurus lepturus	9	0.04	0.1	11.2	6.0-22.0	Pr
Apogonid 5	7	0.04	0.1	5.7	3.5-9.5	Pr,Fl,Po
Parapriacanthus sp.	8	0.04	0.1	6.1	4.0-7.0	Pr,Po
Scomberomorus sp.2	7	0.04	0.1	5.3	2.5-7.0	Pr,Fl
Omobranchus sp	8	0.04	0.1	4.7	3.9-7.5	Pr,Fl
Abudefduf sp.	7	0.04	0.1	5.0	3.1-11.0	Pr,Fl,Po
Labrid 6	8	0.04	0.1	3.9	3.5-4.5	Pr
Gobiid 5	13	0.04	0.1	6.8	4.5-8.5	Po
Liminichthys nitidus	11	0.04	0.2	11.7	11.0-13.0	Po
Platycephalid 1	9	0.04	0.2	6.2	3.0-10.5	Pr,Fl,Po
Carangid 4	10	0.05	0.2	3.7	2.8-5.0	Pr,Fl,Po
Coryphaena hippurus	9	0.05	0.2	8.2	4.5-12.0	Pr,Fl,Po
Labrid 2	11	0.05	0.2	5.6	3.9-7.5	Fl
Lutjanid 1	9	0.05	0.2	4.1	2.5-6.0	Pr,Fl
Umbrina ronchus	12	0.06	0.2	3.5	2.3-4.0	Pr,Fl
Samaris cristatus	12	0.06	0.2	6.8	3.0-11.0	Pr,Fl,Po
Pempheris sp.1	11	0.07	0.2	4.3	2.0-7.0	Pr
Apogonid 3	17	0.07	0.3	4.4	3.0-6.5	Pr,Fl,Po
Lethrinid 1	14	0.07	0.3	4.0	3.0-6.0	Pr,Fl
Cynoglossus sp.3	12	0.07	0.3	9.2	5.0-13.0	Pr,Fl,Po
Lagocephalus inermis	16	0.08	0.3	4.2	2.0-10.0	Pr,Po
Tetraodont 1	17	0.08	0.3	3.0	2.0-3.6	Pr
Pseudorhombus sp.	15	0.08	0.3	7.2	4.3-9.0	Pr,Po
Scorpaenid 5	20	0.09	0.3	6.2	3.0-11.0	Pr,Fl,Po
Apistes carinatus	15	0.09	0.3	5.7	3.8-8.0	Pr,Fl,Po
Stephanolepis auratus	12	0.09	0.3	5.5	3.0-10.0	Pr,Po
Gobiid 16	18	0.10	0.4	4.2	3.0-6.0	Pr,Fl,Po
Scomberoides sp.	14	0.10	0.4	5.7	3.0-14.0	Pr,Fl,Po
Clupeid 1	19	0.10	0.4	4.6	4.0-6.5	Pr
Pempheris sp.2	23	0.12	0.4	3.0	2.5-4.2	Pr
Trachinocephalus myops	27	0.12	0.4	8.4	3.0-39.0	Pr,Fl,Po,Ju
Cynoglossid 1	14	0.12	0.5	9.1	6.0-14.0	Pr,Fl,Po
Gobiesocid 2	28	0.13	0.5	4.5	2.5-7.0	Pr,Fl,Po
Scombrid 2	25	0.13	0.5	3.1	3.0-3.5	Pr

Gobiid 12	31	0.13	0.5	5.4	3.2-7.8	Pr,Po
Lepadichthys sp.1	38	0.15	0.5	5.2	2.5-44.0	Pr,Fl,Po
Sparid 3	30	0.15	0.6	4.1	2.5-11.0	Pr,Fl,Po
Trichonotus marleyi	37	0.15	0.6	12.1	7.0-17.0	Fl,Po
Carangid 1	37	0.20	0.8	4.5	2.0-13.0	Pr,Fl,Po
Mullid 1	36	0.21	0.8	5.4	3.5-8.5	Pr,Fl,Po
Nemipterus sp.	47	0.24	0.9	4.6	3.2-6.0	Pr,Fl,Po
Istiblennius sp.	50	0.28	1.0	5.7	2.5-16.0	Pr,Fl,Po
Platycephalid 2	3	0.01	<0.1	7.5	3.5-10.0	Pr,Po
Platycephalid 3	1	<0.01	<0.1	3.2	3.2	Pr
Dactyloptena orientalis	2	0.01	<0.1	3.1	2.5-3.7	Pr
Epinephalus sp.	1	0.01	<0.1	15.0	15.0	Po
Cephalopholis sp.	1	0.01	<0.1	10.0	10.0	Po
Pseudochromid 2	1	0.01	<0.1	7.5	7.5	Po
Priacanthid 1	2	0.01	<0.1	5.3	3.5-7.0	Pr,Po
Rhabdamia gracilis	2	0.01	<0.1	11.9	4.7-19.0	Fl,Ju
Pseudamia gelatinosa	3	0.01	<0.1	6.0	3.0-9.0	Pr,Po
Apogon sp.2	1	<0.01	<0.1	7.2	7.2	Po
Apogon sp.3	1	0.01	<0.1	4.5	4.5	Po
Apogonid 7	2	0.01	<0.1	10.3	10.0-10.5	Po
Apogonid 8	1	0.01	<0.1	3.6	3.6	Pr
Apogonid 9	1	<0.01	<0.1	4.2	4.2	Pr
Apogonid 10	1	<0.01	<0.1	3.8	3.8	Fl
Scombrops boops	1	0.01	<0.1	8.5	8.5	Po
Haemulid 1	2	0.01	<0.1	4.9	4.8-5.0	Pr
Lutjanid 5	1	<0.01	<0.1	3.5	3.5	Pr
Sparid 2	1	<0.01	<0.1	5.9	5.9	Po
Mullid 2	1	<0.01	<0.1	13.0	13.0	Po
Chactodontid 1	1	0.01	<0.1	3.0	3.0	Pr
Bramid 1	1	<0.01	<0.1	5.5	5.5	Fl
Elagatis bipinnulata	1	0.01	<0.1	5.2	5.2	Fl
Decapterus sp.1	1	0.01	<0.1	4.0	4.0	Fl
Caranx sexfaciatus	1	0.01	<0.1	6.5	6.5	Po
Carangid 2	1	<0.01	<0.1	3.2	3.2	Pr
Carangid 5	1	0.01	<0.1	7.0	7.0	Po
Pempherid 1	1	<0.01	<0.1	3.4	3.4	Pr
Pomacentrus sp.	2	0.01	<0.1	5.1	4.0-6.2	Pr,Po
Xyrichthys sp.1	3	0.01	<0.1	10.7	9.0-12.0	Po
Xyrichthys sp.2	2	0.01	<0.1	11.0	10.0-12.0	Po
Labrid 1	1	<0.01	<0.1	11.0	11.0	Po
Labrid 3	2	0.01	<0.1	6.5	6.5	Po
Labrid 4	1	<0.01	<0.1	9.0	9.0	Po
Labrid 5	2	0.01	<0.1	7.0	6.0	Pr,Po
Labrid 7	1	0.01	<0.1	8.0	8.0	Pr
Scarid 1	3	0.01	<0.1	7.3	5.8-10.0	Po
Scarid 2	1	0.01	<0.1	8.0	8.0	Po
Uranoscopid 1	1	0.00	<0.1	3.3	3.3	Pr
Blenniid 7	1	0.01	<0.1	4.0	4.0	Pr
Tripterygiid 4	1	<0.01	<0.1	4.0	4.0	Pr
Embolichthys mitsukurii	1	<0.01	<0.1	20.0	20.0	Po
Gobiid 15	2	0.01	<0.1	6.1	6.0-6.2	Po
Gobiid 17	1	0.01	<0.1	8.0	8.0	Po
Gobiid 18	1	0.01	<0.1	6.0	6.0	Po
Gobiid 19	1	<0.01	<0.1	3.5	3.5	Pr
Gobiid 20	1	<0.01	<0.1	5.0	5.0	Po
Gempylus serpens	2	0.01	<0.1	5.5	4.0-7.0	Pr,Po
Gempylid 2	2	0.01	<0.1	3.5	3.2-3.8	Pr,Fl
Scombrid 3	2	0.01	<0.1	4.0	3.9-4.1	Pr
Scombrid 5	1	0.01	<0.1	3.0	3.0	Pr
Cynoglossid 2	2	0.01	<0.1	6.4	4.8-8.0	Pr,Po
Soleid 3	1	0.01	<0.1	11.0	11.0	Po
Balisitd 1	2	0.01	<0.1	4.5	3.0-6.0	Pr,Po
Monacanthid	1	0.01	<0.1	2.8	2.8	Pr
Lactoria	1	<0.01	<0.1	11.0	11.0	Po
Amblyrynchotes honckenii	2	0.01	<0.1	8.5	5.0-12.0	Fl,Po
Oceanic taxa						
Stomias sp.	7	0.04	0.1	11.5	7.0-19.0	Pr,Fl,Po
Chauliodus sp.	1	<0.01	<0.1	12.0	12.0	Fl
Astronestes sp.	3	0.01	<0.1	11.8	9.0-17.0	Po
Photonectes parvimanus	1	<0.01	<0.1	28.0	28.0	Po
Melanostomid 1	1	0.01	<0.1	9.0	9.0	Pr
Pollichthys mauli	4	0.02	0.1	5.8	4.6-7.0	Pr,Fl,Po
Diplophos taenia	2	0.01	<0.1	27.5	23.0-32.0	Po
Gonostoma atlanticum	3	0.01	<0.1	6.2	5.0-7.0	Pr,Po
Sternophichthyid	3	0.01	<0.1	4.5	4.0-5.5	Pr

Scopelosaurus sp.	24	0.09	0.3	7.0	2.5-12.5	Pr
Lestidium atlanticum	4	0.02	0.1	8.8	6.0-12.0	Pr,Fl
Paralepid	8	0.04	0.1	7.6	5.0-10.0	Pr,Fl
Dinematichthys sp.	1	0.01	<0.1	8.0	8.0	Fl
Histrio histrio	2	0.01	<0.1	3.2	2.5-3.9	Po
Ogocephalid	1	<0.01	<0.1	6.0	6.0	Po
Ceratiid 1	2	0.01	<0.1	4.3	3.8-4.8	Po
Trachipterid 1	4	0.02	0.1	7.7	6.5-9.4	Pr
Melamphaes sp.	1	0.01	<0.1	6.5	6.5	Po
Champsodon capensis	2	0.01	<0.1	5.8	5.0-6.5	Fl,Po
Bemprops sp.	13	0.06	0.2	6.0	6.0	Pr
Amarsipus sp.	4	0.03	0.1	4.4	3.0-5.2	Pr,Fl,Po
Cubiceps sp.	2	0.01	<0.1	3.5	3.5	Pr
Psenes sp.	9	0.05	0.2	7.9	5.0-10.0	Fl,Po
Nomeid 1	2	0.01	<0.1	6.5	6.0-7.0	Fl,Po
Nomeid 2	2	0.01	<0.1	4.7	4.5-4.8	Fl
Chloropthalmid	1	<0.01	<0.1	8.9	8.9	Fl
Ceratoscopelus sp.	1	0.01	<0.1	6.0		Pr,Fl,Po
Diaphus sp.1	2	0.01	<0.1	3.8		Pr,Po
Diaphus sp.3	3	0.03	0.1	4.6	3.0-6.0	Pr,Po
Lampanyctus alatus	8	0.03	0.1	4.0	3.1-4.9	Pr,Fl
Lampanyctus B	1	<0.01	<0.1	6.5		Pr,Po
Symbolo evermanni	1	<0.01	<0.1	6.8		Pr,Fl,Po
Myctophum sp.	7	0.05	0.2	5.3	4.0-6.5	Po
Diaphus mollis	13	0.06	0.2	4.6	3.5-5.5	Pr,Fl,Po
Triphoturus nigrescens	11	0.04	0.2	4.6	3.0-6.0	Pr,Fl
Diaphus brachycephalus	6	0.02	0.1	5.2	4.0-6.2	Pr,Fl,Po
Lampadena sp.	23	0.09	0.3	5.9	3.0-8.0	Pr,Fl,Po
Myctophum selenops	5	0.02	0.1	5.0	3.5-6.5	Pr,Fl,Po
Myctop nitidum	2	0.01	<0.1	5.5	5.0-6.0	Pr,Fl
Ceratoscopelus warmingii	7	0.04	0.1	6.1	4.5-8.0	Po
Lampanytus pusillus	1	<0.01	<0.1	4.4		Pr,Fl,Po
Lobianchia gemellari	3	0.01	0.1	5.8	2.9-9.0	Po
Myctophum asperum	1	0.01	<0.1	4.8		Po
Lampanyctus D	1	0.01	<0.1	8.0		Pr,Fl,Po
Lampanyctid 1	4	0.02	0.1	4.5	3.0-6.0	Fl
Myctophid 14	1	<0.01	<0.1	6		
Taanichthys minimus	1	0.01	<0.1	5.0		Pr,Po