S. Afr. J. mar. Sci. 21: 19–39
1999

COMPOSITION, ABUNDANCE AND SEASONALITY OF FISH LARVAE IN THE MOUTH OF DURBAN HARBOUR, KWAZULU-NATAL, SOUTH AFRICA

S. A. HARRIS† and D. P. CYRUS**

Ichthyoplankton samples were collected every six weeks at night on consecutive ebb and flood tides over an 18-month period (June 1991–December 1992) at surface, middle and bottom depths near the entrance of Durban Harbour to investigate the composition, abundance, seasonality and developmental stages of fish larvae in the harbour. In all, 8 797 fish larvae, representing 144 species and 64 families were collected. The Clupeidae and Gobiidae were the dominant families, representing 30 and 15% of the total catch respectively. The most abundant larvae were the blueline herring *Herklotsichthys quadrimaculatus*, which contributed 29.7% of the total catch. Larvae of estuarine-independent species dominated the total catch, both in terms of density (78%) and number of species (81%). In all, 28 species dependent on estuaries at some stage in their life cycle were recorded; of these 13 were species totally dependent on estuaries. Temperature and salinity accounted for 31% of the variation in larval densities of estuarine-dependent species. Turbidity was a significant variable for estuarine-independent species, larval densities of the abundant species being negatively correlated to turbidity. Larval density peaked mainly in August 1992 (winter), with a mean larval density of 118 larvae·100m^{-3}. Larvae of estuarine-associated species were mainly at the flexion and postflexion developmental stages, whereas most larvae of estuarine-independent species were at preflexion and flexion stages. Larval densities of certain estuarine-associated species (e.g. *Argyrosomus* sp.) were significantly higher in bottom samples, mainly on flood tides but also on ebb tides, suggesting that selective tidal stream transport is a recruitment mechanism used by these species. The impact of harbour development is shown by the dominant marine component of the larval fish assemblage in the harbour. However, despite the seminatural estuarine environment of Durban Harbour, the high species diversity of fish larvae in the system indicates that the harbour is in a relatively good ecological condition.

Durban Harbour is situated at 29°53′S and 31°00′E on the KwaZulu-Natal coast and is one of the busiest shipping ports in Africa. Prior to its development in the late 1800s, the system was called "Port Natal" and was described as a large bay with freshwater flowing into it (Holden 1855). The bay was permanently open to the sea and shallow (< 3 m), with the depth varying depending on the state of the sandbar in the entrance channel (Hay *et al.* 1995). Two rivers, the Umbilo and Mhlatuzana, enter the bay through canalized inlets on the south-west side of the harbour and supply minimal freshwater input, 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 shoreline perimeter of some 27 km (Begg 1978, Forbes *et al.* 1994). In its pristine state, the bay of Port Natal must have functioned as a typical estuarine and nursery habitat with a diverse ichthyofauna. Currently, Durban Harbour is better defined as an "embayment" (Begg 1978), because the system is tidally dominated with near-marine salinities. 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).

Early biological surveys of the bay (Day and Morgans 1956, Wallace 1975a, b) found that, despite the impact of the harbour developments, a surprisingly rich ichthyofauna persisted, with many of the fish being euryhaline species typical of other KwaZulu-Natal estuaries. More recent studies show that, despite the prevalent stenohaline marine component, many of the fish species found in the bay are still euryhaline estuarine species (Hay *et al*. 1993, Beckley *et al.* 1994, Cyrus and Forbes 1994, 1996, Graham 1994, Guastella 1994), indicating that Durban Harbour still serves as an important nursery site for these fish species. All previous fish surveys have examined only adult and juvenile life-history stages (Day and Morgan 1956, Wallace 1975 a, b, Begg 1978, Hay *et al*. 1993, Beckley *et al*. 1994, Cyrus and Forbes 1994, 1996; Guastella 1994), with no studies on the larval life-history stages, with the exception of some non-quantitative work by A. D. Connell, CSIR, pers. comm.). To further understanding of the utilization of estuarine nursery areas by estuarine-associated fish

* Coastal Research Unit of Zululand, University of Zululand, Private Bag X1001, KwaDlangezwa 3886, KwaZulu-Natal, South Africa
† Present address: Black & Veatch Africa, P.O. Box 30705, Braamfontein 2017, Johannesburg, South Africa. E-mail: harriss@bv.co.za

Manuscript received: November 1997

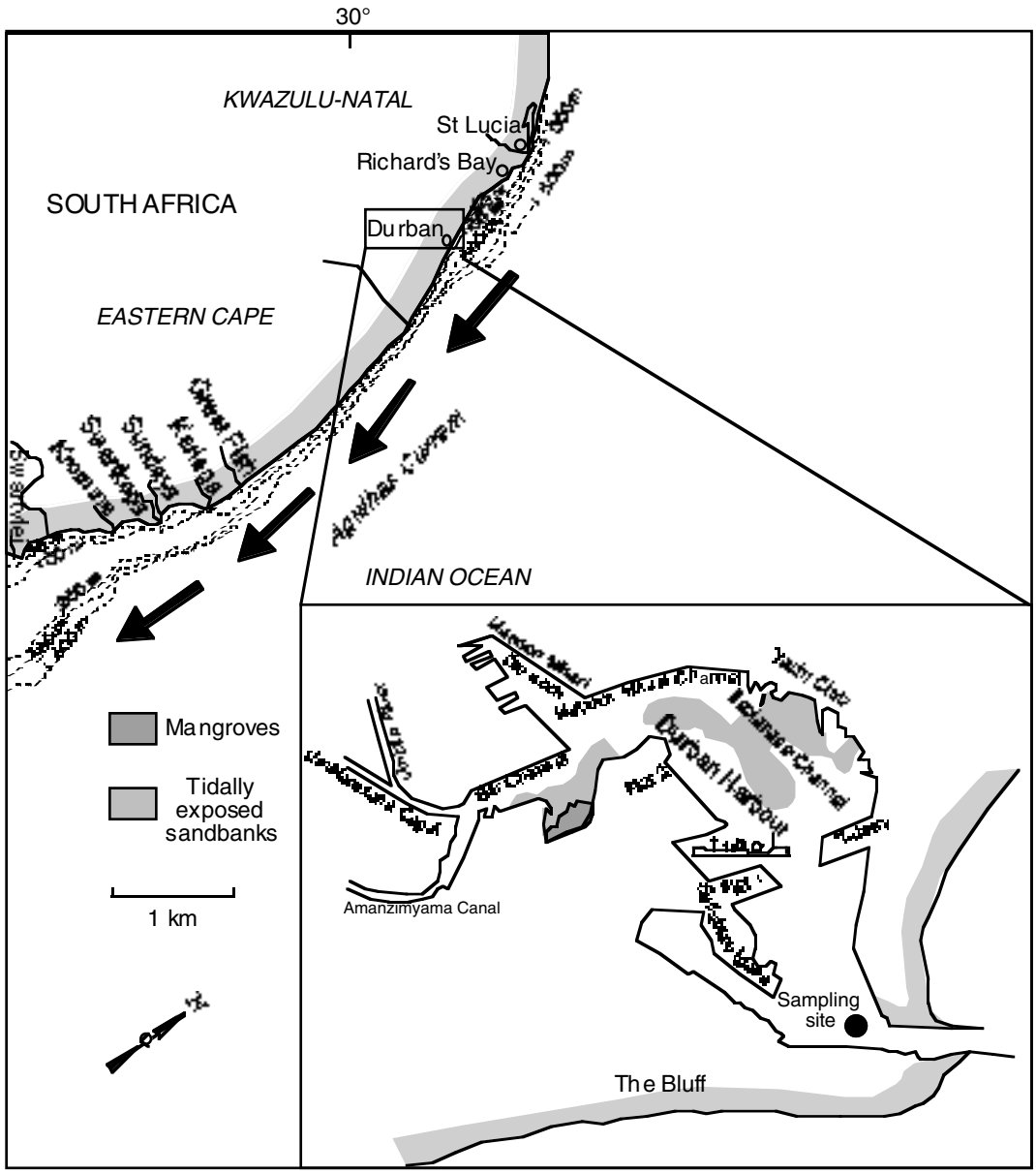

Fig. 1: Location of Durban Harbour on the KwaZulu-Natal coast, and the sampling site near the entrance of the harbour

species, it is important to examine the early life-history stages of these fish (Whitfield 1989). Marine fish species utilizing estuaries as nurseries are recruited at an early life-history stage, particularly as postflexion larvae (Whitfield 1989, Gaughan *et al.* 1990, Harrison and Whitfield 1990, Tzeng and Wang 1992, Neira *et al.* 1992, Harris and Cyrus 1995, 1997, Harris *et al.* 1995).

The present study investigates the composition, abundance, seasonality and developmental stages of fish larvae occurring near the Durban Harbour entrance,

Table I: Summary of the sampling programme at the study site in Durban Harbour

Sampling programme	Details
Sampling dates (spring tides)	June 1991 – Dec. 1992
Number of sampling trips	13
Mean (± 1*SD*) sampling depths (m)	
Middle depth	3.7 ± 1.4
Bottom depth	8.5 ± 2.5
Number of samples	
Ebb tide	110
Flood tide	119
Mean (± 1*SD*) volumes of water filtered (m^3)	
Surface	108.0 ± 33.5
Middle	113.8 ± 35.4
Bottom	106.1 ± 33.8

i.e. the lower reaches of the estuarine system. Estuarine-associated species were identified and discussed in terms of recruitment into the harbour.

MATERIAL AND METHODS

Sampling programme

Ichthyoplankton samples were collected at a sampling site in the dredged channel near the entrance of Durban Harbour (Fig. 1). Samples were collected approximately every six weeks from June 1991 to December 1992, over spring tides at night, on consecutive ebb and flood tides (see Table I). A 500-µm mesh plankton net (57-cm mouth diameter and 2.5 m long), equipped with a flowmeter (General Oceanics), was towed about 10 m behind a launch into the current (average speed 1 $m \cdot s^{-1}$). The depth fished was controlled by varying the length of the rope and the number of weights and floats. Three series of three hauls were taken at approximately $1\frac{1}{4}$-h intervals at the surface, middle and near-bottom depths. The depths of the middle and bottom samples varied depending on the state of the tide. Samples were preserved in 4% buffered formalin. Temperature (°C), salinity ($\times 10^{-3}$) and turbidity (nephelometric turbidity units – NTU) were measured during the collection of each sample.

Laboratory procedures

Larvae were identified to the lowest possible taxon according to Fahay (1983), Leis and Rennis (1983), Moser *et al*. (1984), Smith and Heemstra (1986), Okiyama (1988) and Leis and Trnski (1989). Fish body lengths were measured (notochord length in preflexion and flexion larvae and standard length in postflexion larvae) 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 the beginning of squamation, at which stage the fish becomes a juvenile (Kendall *et al.* 1984). Terminology to designate larval developmental stages follows Kendall *et al*. (1984) and includes: leptocephalus (Le), preflexion (Pr), flexion (Fl), postflexion (Po) and juvenile (Ju). Older larvae are defined as postflexion, and younger larvae as both preflexion and flexion (Leis 1991).

Estuarine-association categories

For the purpose of this study, the term "estuarine-dependent" refers to those fish species for which estuaries form an essential habitat for at least one stage of their life cycle (Blaber *et al.* 1989). Each taxon was categorized according to the degree to which the species is dependent on estuaries in its life cycle. All species were then grouped into one of the following three groups (adapted from Whitfield 1994a, b):

Estuarine-dependent species

Ia Estuarine species which only breed in estuaries, e.g. estuarine round herring *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 need estuaries as conduits to and from freshwater catchment areas (i.e. require a freshwater phase in their development), e.g. longfin eel *Anguilla mossambica.*

Partially estuarine-dependent species

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

IIb Euryhaline marine species which usually breed at sea, but the juveniles occur either in estuaries and/or at sea, e.g. groovy mullet, *Liza dumerilii*;

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

Vb Facultative catadromous species which do not require a freshwater phase in their development, but juveniles are often strongly associated with estuaries, e.g. oxeye tarpon *Megalops cyprinoides.*

Table II: Total catch, percentage composition, body length and development stage per estuarine-association group for all fish larvae collected at the study site in Durban Harbour

Estuarine-associated group		Ranking	Total catch			Body length (mm)		Developmental stages	Presence	Juvenile and adult present[A]
Family	Species		Number	Mean density (number·100^{-3})	% of total catch	Mean	Range			
ESTUARINE RESIDENTS										
					Estuarine-dependent					
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	+
					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	+

(continued)

Table II: (*continued*)

Estuarine-associated group		Ranking	Total catch			Body length (mm)		Developmental stages	Presence	Juvenile and adult present[A]
Family	Species		Number	Mean density (number·100^{-3})	% of total catch	Mean	Range			
ESTUARINE-INDEPENDENT[B]										
					Reef and shore taxa					
Clupeidae	*Herklotsichthys quadrimaculatus*	1	2 748	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	
					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 = 8 797
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
Le = leptocephali; Ys = yolk sac; Pr = preflexion; Fl = flexion; Ju = juvenile; F = flood tide; E = ebb tide
* Abundant
** Very abundant

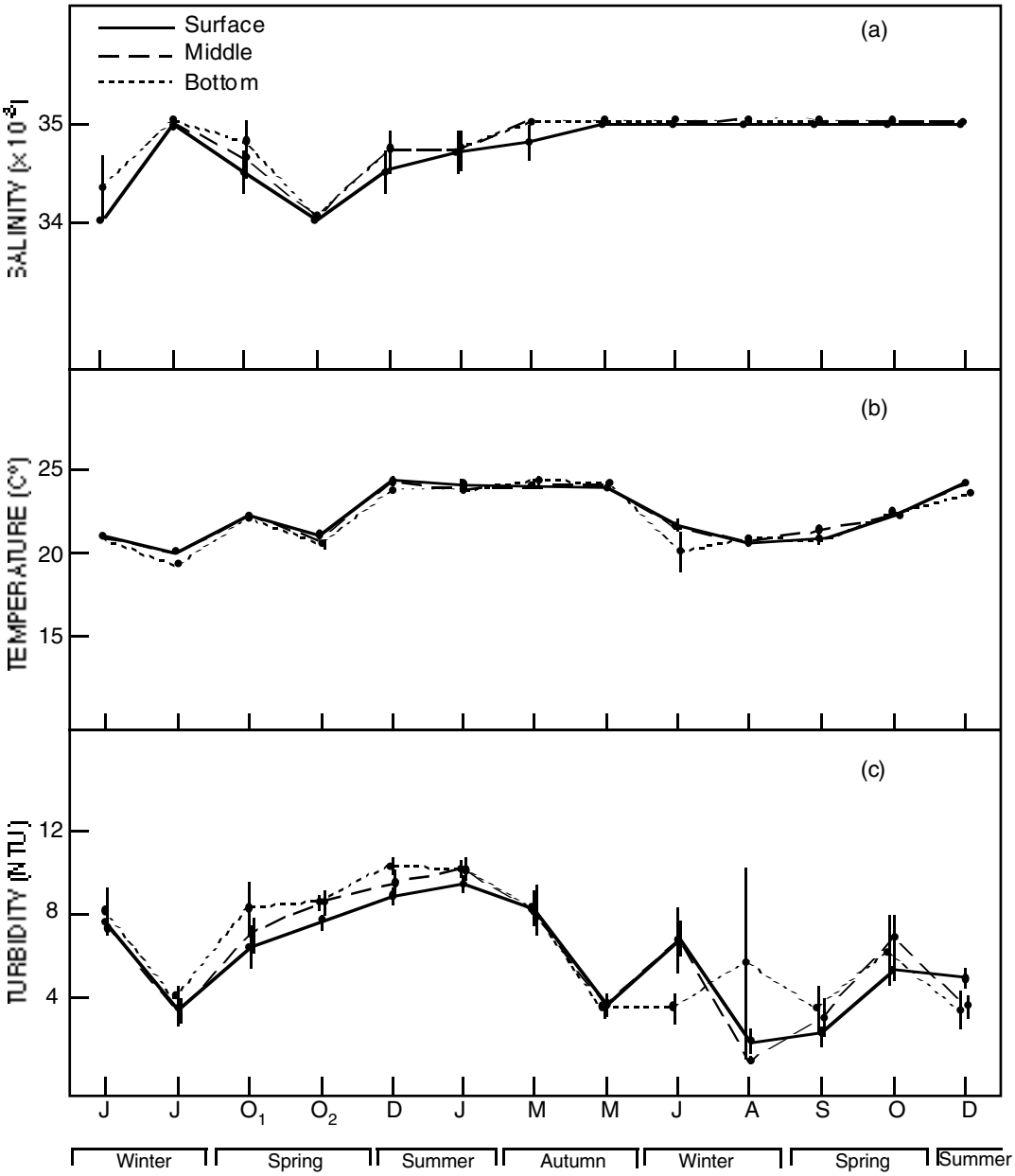

Fig. 2: Mean monthly variations (± 1*SE*) of (a) salinity, (b) temperature and (c) turbidity for surface, middle and bottom samples in Durban Harbour during the study period

Estuarine-independent species

IV Euryhaline freshwater species, e.g. barebreast goby *Silhouetta sibayi*;

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

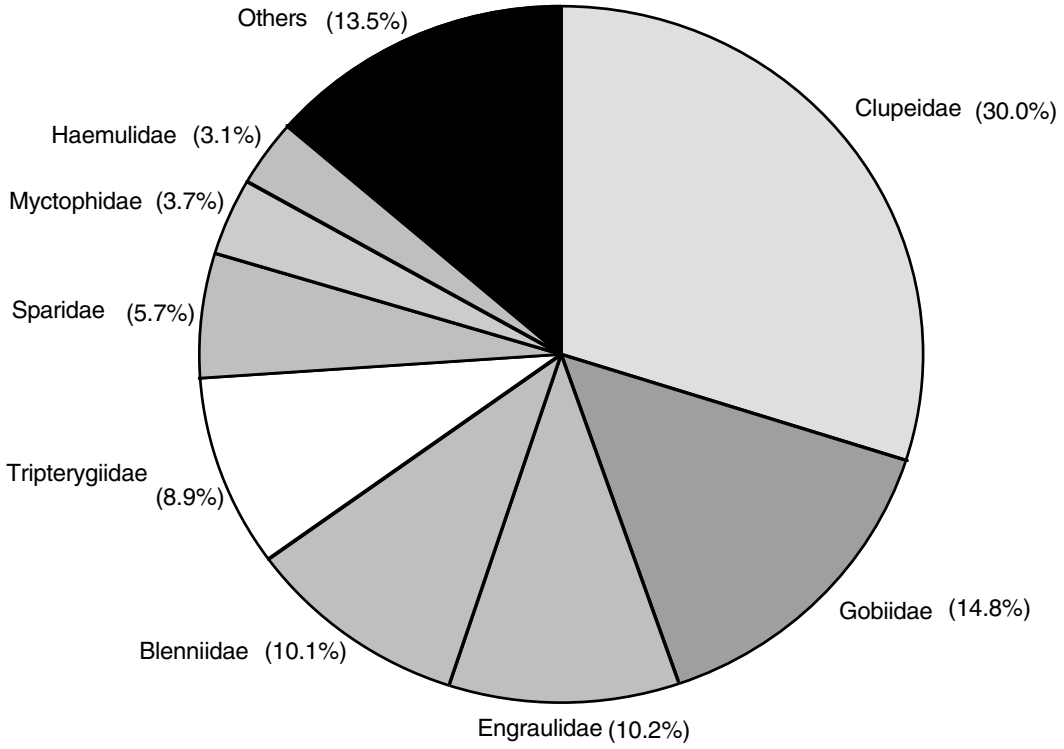

Fig. 3: Percentage contribution of the dominant families for all species collected during the study

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

Analyses of data

For all statistical analyses, a significance level of $p < 0.05$ was used. Before testing, larval density data were log-transformed [$\log_{10}$ $(x + 1)$] to conform to normality and homogeneity of variances. Where necessary, turbidity and salinity data were also log-transformed. Significant differences in environmental variables (current velocity, salinity, temperature and turbidity) and density of fish larvae between surface, middle and bottom samples, and between sampling dates were detected by means of a two-way or three-way analysis of variance (ANOVA – Tukey test). Duncan's Multiple Range test was used to identify where significant differences occurred. Multiple linear and stepwise-regressions were used to ascertain whether the environmental variables showed any statistical relationship with larval densities.

The total number of larvae for all taxa caught in all the samples (surface, middle and bottom) was recorded and converted to density (number of larvae·100m^{-3}). These adjusted numbers were used to calculate the percentage contribution of each species to the total catch. The total mean catch (Table II) is the sum of the mean densities each month divided by the number of sampling periods.

RESULTS

Environmental variables

During the study period (June 1991–December 1992) water conditions at the sample site in Durban Harbour were essentially marine. The mean monthly salinity reached a minimum of 34.0×10^{-3} in June and late October 1991 and a maximum of 35.0×10^{-3} in July 1991 and from May to December 1992 (Fig. 2). No

Table III: Stepwise regression statistics of larval fish densities versus environmental variables per estuarine-association group and most abundant species in each group collected at the study site in Durban Harbour (adj = R^2 coefficient of determination; R = correlation coefficient; F = F statistic)

Estuarine-association group	AdjR^2	R	F	Significant variables
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.	*NS*	*NS*	*NS*	*NS*
Stolephorus holodon	*NS*	*NS*	*NS*	*NS*
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**
Blennid 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*
All taxa	0.22	0.47	21.91***	sa***; −tu***; −te**

sa = salinity; te = temperature; tu = turbidity
* $p < 0.05$
** $p < 0.01$
*** $p < 0.0001$
NS = not significant ($p > 0.05$)

significant differences in salinities were found between ebb and flood tides or with depth, but significant differences were found between sampling dates ($p < 0.0001$). Mean monthly water temperature reached a maximum of 24.3°C in December 1991 (summer, Fig. 2) and was lowest during winter in July 1991 (19.2°C) and June 1992 (20.0°C). Temperature values were not significantly different between ebb and flood tides, but were significantly higher at surface and middle depths than at bottom depths ($p < 0.0001$), and differed significantly between seasons ($p < 0.0001$). Turbidity peaked in January 1992 (10.2 NTU) and was at its minimum (1.0 NTU) in August 1992 (Fig. 2). Turbidity was significantly higher on ebb tides ($p < 0.05$) and was usually higher in bottom and middle water depths, although this was not significant. The overall range in turbidities was small, but mean turbidities were significantly different between months ($p < 0.0001$).

Assemblage composition and relationships to environmental variables

In all, 8 797 fish larvae, representing 64 families and 144 species, were collected between June 1991 and December 1992 (Table II and Appendix). Clupeidae was the most abundant family, comprising 30% of the total catch (Fig. 3), followed by Gobiidae (14.8%), Engraulidae (10.2%), Blenniidae (10.1%), Tripterygiidae (8.9%), Sparidae (5.7%), Myctophidae (3.7%) and Haemulidae (3.1%). Other families contributing 1% and more 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, followed by *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*, *Solea bleekeri*, *Argyrosomus* sp. and *Scopelopsis multipunctatus* each contributed between 1 and 4% of the total (Table II).

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 was species-specific (Table III). With all species in the regression model, 22% of the variation in larval densities was accounted for by salinity, turbidity and temperature, with densities being greater at higher salinities and lower turbidities and temperatures. Temperature and salinity accounted for 31% of the variation in larval densities of estuarine-dependent species, whereas densities were greater at lower temperatures and higher salinities ($p < 0.001$). Larval densities of the sparid *R. sarba,* an estuarine-dependent species, were

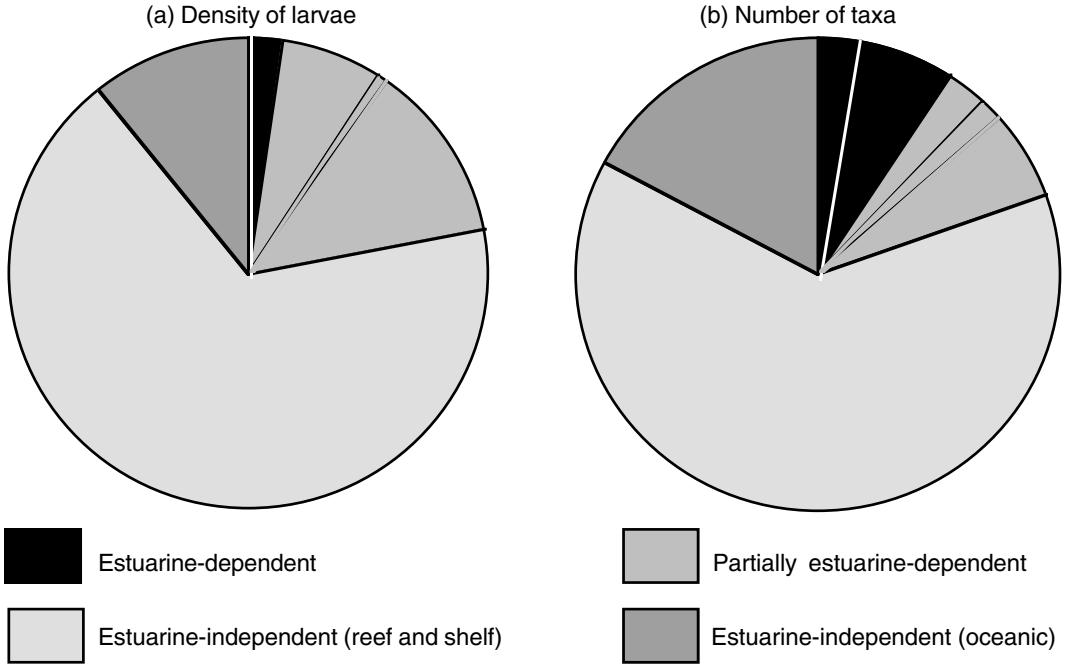

Fig. 4: Percentage contribution of the estuarine-association categories, in terms of (a) density of larvae and (b) number of taxa, for all species sampled during the study

significantly correlated to salinity and temperature ($p < 0.001$) and turbidity ($p < 0.05$). In contrast, densities of the haemulid *P.commersonnii*, also an estuarine-dependent species, were only correlated to temperature ($p < 0.001$). There was no correlation between environmental variables and larval densities for species partially dependent on estuaries, except for *S. bleekeri*, for which temperature was the most significant variable ($p < 0.001$). Density variations of species not dependent on estuaries were explained by all three environmental variables, to varying degrees (4–23% of the model, Table III). Salinity was positively correlated to larval densities of the dominant estuarine-independent species, whereas temperature and turbidity were negatively correlated. (Table III).

Estuarine association

Larvae of species that are marine spawners and are not dependent on estuaries (Categories IIIa, IIIb) dominated the total catch, both in terms of density (78.0%) and number of species (80.6%, Fig. 4). In all, 28 species dependent on estuaries to some degree (Categories I and II) were recorded and contributed to 22.0% of the total density. Of the 28 species, 13 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.

Temporal and spatial trends in larval fish density

Densities of all species generally peaked in August 1992 (118 larvae·100m^{-3}) and was lowest in early October 1991 (2 larvae·100m^{-3}, Fig. 5a). The mean density of estuarine-dependent species was largest in June 1992 (18 larvae·100m^{-3}) and lowest in early October 1991 (0.2 larvae·100m^{-3}, Fig. 5b). The peak in June 1992 was a result of the presence of larval *R. sarba* and *P.commersonnii,* with the former species contributing to a smaller peak in July 1991 (14 larvae·100m^{-3}, Fig. 6). Densities of partially estuarine-dependent species were highest in late October 1991 and December 1992, reaching a maximum of 20 larvae·100m^{-3} (Fig. 5c), consisting mainly of

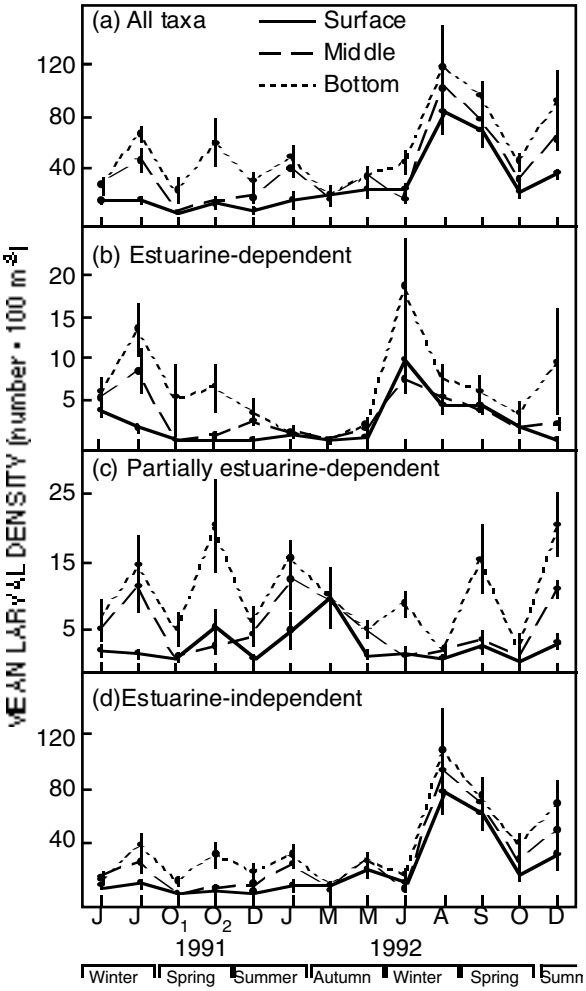

Fig. 5: Mean monthly variations in larval density (± 1*SE*) in the surface, middle and bottom samples for (a) all taxa, (b) estuarine-dependent species, (c) partially estuarine-dependent species and (d) estuarine-independent species

S. holodon (Fig. 6). Estuarine-independent species were most abundant in August 1991 (109 larvae·100m^{-3}) and least abundant in early October 1991 (2 larvae·100m^{-3}, Fig. 5d). The peak in abundance in August 1992 was mainly as a result of the presence of *H. quadrimaculatus* and, to a lesser extent, Blenniid 1, Gobiid 12 and Tripterygiid 1 (Fig. 6).

Three-way ANOVAs showed that larval densities of the abundant estuarine-associated species, (except *R. sarba)* had significantly higher densities on flood tides (Table IV). All six of those species had significantly higher densities in middle and bottom strata ($p > 0.001$) for both flood and ebb tides (Fig. 9). This was particularly evident for the sciaenid *Argyrosomus* sp., whose larvae were abundant on flood tides and near the seabed, with few larvae in surface waters on the ebb tides (Fig. 9). Of the five most abundant estuarine-independent species, only two (Tripterygiid 1 and Gobiid 12) showed some trend with tide, with significantly higher densities on ebb tides ($p < 0.05$, Table IV). Estuarine-independent species (except for Gobiid 12 and *Scopelopsis multipunctatus*) densities were highest near the seabed on either flood or ebb tides (Table IV, Fig. 9). Although month had a significant effect for all groups and individual species, the mean squares were relatively small (Table IV). The tide × depth interaction was significant for *S. bleekeri* ($p < 0.01$), *Argyrosomus* sp. and *S. holodon* ($p < 0.05$), which are all partially estuarine-dependent. The tide × month and depth × month interactions were significant, particularly for *P. commersonnii, S. bleekeri, Argyrosomus* sp., Tripterygiid 1, Blenniid 1 and *H. quadrimaculatus* ($p < 0.001$, Table IV). The mean squares for all the interactions were generally small ($p < 0.50$).

Developmental stages

Developmental stages in the estuarine-dependent group were predominantly young larvae (65.0% of the total), with 30.2% of the larvae at postflexion stages (Fig. 7). The leptocephalus larvae from the estuarine-dependent group were *Elops machnata*. Marine spawners, which are 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 comprised *H. quadrimaculatus,* the juvenile stages of Blennid 6, *Caranx sexfasciatus*, Melanostomiid 1 and *Schindleria praematura*, and the adult stage of *S. praematura* (see Table II and Appendix). The leptocephali in this category were eel species.

The proportions of developmental stages changed between months.Young larvae (preflexion and flexion) were most abundant in late October 1991 and from August to December 1992, i.e. late winter, spring and early summer (Fig. 8). Postflexion larvae were dominant in December 1991 and in March 1992. The leptocephali were present 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.

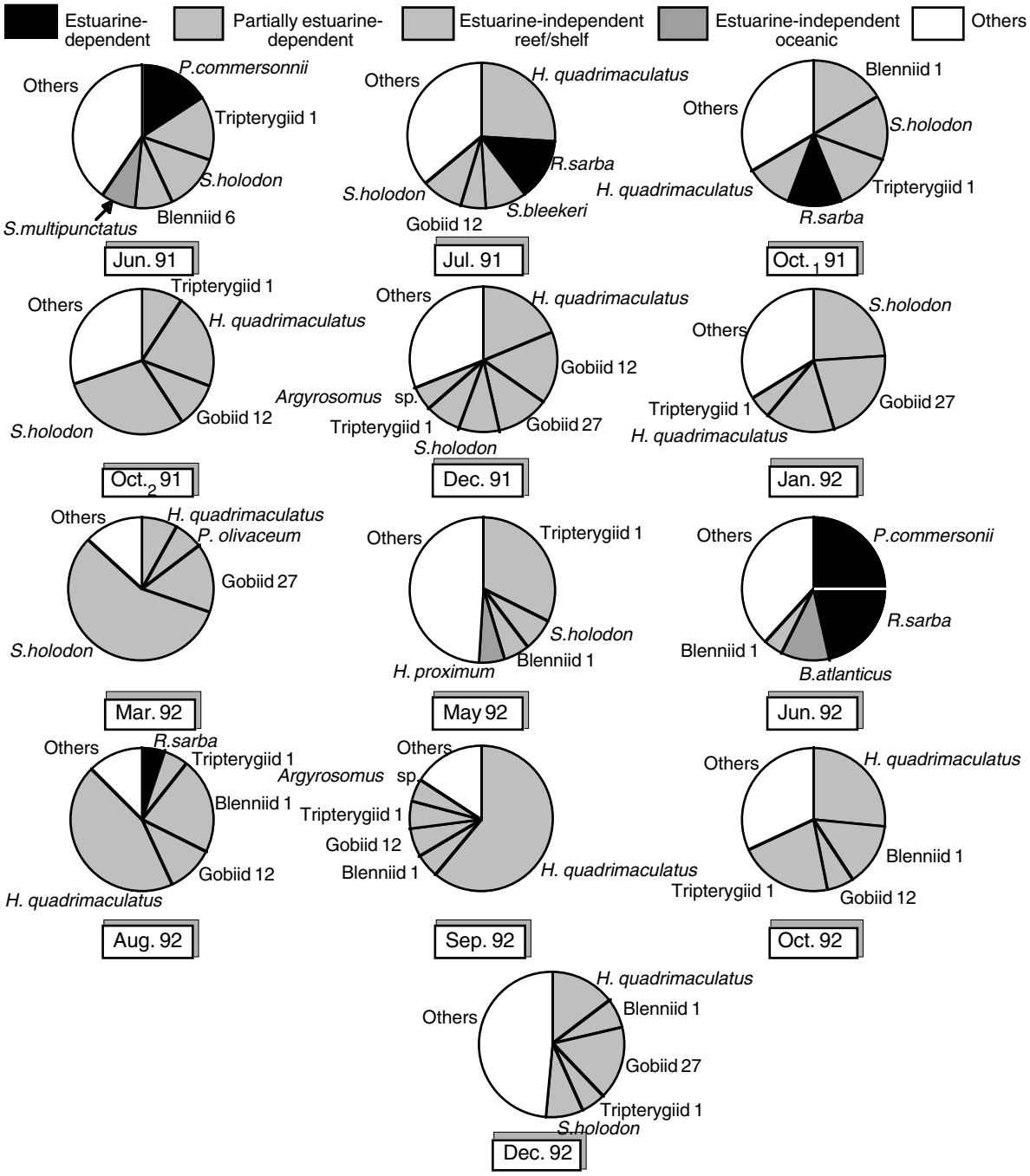

Fig. 6: Percentage contribution of the most abundant species, for each estuarine association category, in the total catch sampled each month in Durban Harbour

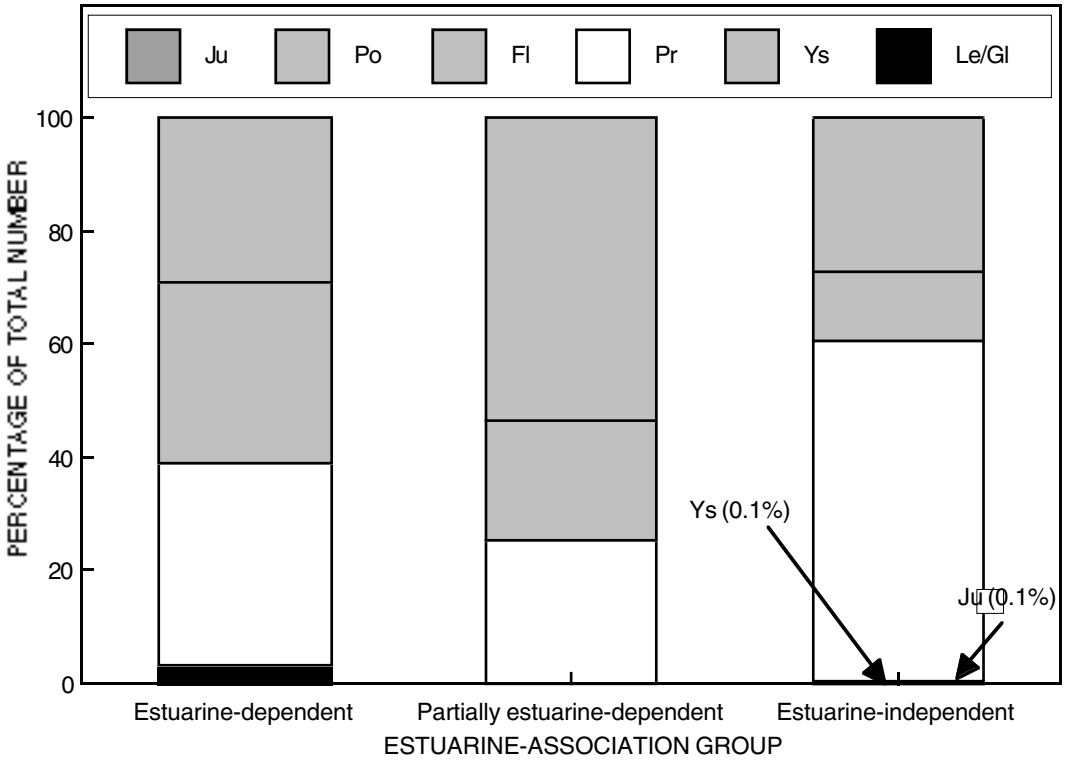

Fig. 7: Percentage composition of the different developmental stages of all larvae for each estuarine-association category, (Le/Gl = leptocephalus/glass eel, Ys = yolk sac, Pr = preflexion, Fl = flexion, Po = postflexion, Ju = juvenile)

The proportion of developmental stages did not vary with tide or depth for all the estuarine-association categories (Fig. 9). Young and old larvae of two of the most abundant estuarine-dependent species, *R. sarba* and *P. commersonnii*, were collected on both flood and ebb tides and throughout the water column (Fig. 9). A similar situation was found for partially estuarine-dependent species, except that only preflexion larvae of *Argyrosomus* sp. were collected in the surface samples on the ebb tide.

DISCUSSION

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 were euryhaline estuarine species typical of other estuaries in KwaZulu-Natal (Wallace 1975a). More recent surveys in the harbour have shown that fish are still abundant, but fewer species are present (Hay *et al.* 1993, Beckley *et al.* 1994, Cyrus and Forbes 1994, 1996, Graham 1994, Guastella 1994). The most abundant species, as juveniles and/or adults, which were recorded in those surveys were *P. commersonnii*, *R. sarba, Acanthopagrus berda, Argyrosomus hololepidotus* (now *A. japonicus* – Griffiths and Heemstra 1995), *Leiognathus equula, Gerres filamentosus, Hilsa kelee* and mugilid spp. Wallace (1975a) suggested that the fish assemblage in Durban Harbour is merely an extension of the marine inshore population because the species composition was representative of the nearshore community. This was confirmed by the above-mentioned studies, as well as the present study, in which 81% (116 species) of all the species collected and 78% of the total

Table IV: Mean squares and significance levels for three-way ANOVA of densities of the most abundant species in each estuarine-association group collected at the study site in Durban Harbour

Estuarine-association group	Main effects			Two-way interactions		
	Tide (F/E)[A] (*df* = 1)	Depth (S,M,B)[B] (*df* = 2)	Month (1–12)[C] (*df* = 11)	Tide × Depth (*df* = 2)	Tide × Month (*df* = 11)	Depth × Month (*df* = 22)
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	10.42*(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
All taxa	0.1	2.87***(B>M>T)	2.06***	0.10	0.21*	0.19**

[A] Tide where densities are significantly higher is indicated in parenthesis. F = flood tide; E = ebb tide
[B] Depths where densities are highest are indicated in parenthesis and Figure 5 (groups only). S = surface; M = middle; B = bottom
[C] Months where densities are highest are indicated in Figure 5 (groups only)
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$
df = degrees of freedom

abundance were marine stragglers. Compared with the juvenile and adult fish assemblage, larvae of different species dominated the catch (*H. qaudrimaculatus*, *S. holodon* and Blenniid 1), with larvae of *P. commersonnii*, *A. berda, Argyrosomus* sp. and *L. equula* being relatively abundant (Table II). Mugilids are one of the most abundant fish species in KwaZulu-Natal estuaries (Wallace 1975a, Whitfield 1994a), particularly during the juvenile stage of their life cycle. Mugilid larvae were relatively abundant in Durban Harbour (ranked 18th overall), but they have not been found in large numbers in other large KwaZulu-Natal estuaries, e.g. St Lucia Estuary (Harris and Cyrus 1995), or in Richards Bay Harbour (Harris and Cyrus 1997). However, mugilid larvae were abundant in the surf zone adjacent to the St Lucia Estuary mouth (Harris and Cyrus 1996), suggesting that, in KwaZulu-Natal, mullet species enter the estuarine habitat at a later developmental stage.

Kob (*Argyrosomus* spp.) are important recreational and commercial fish species in South Africa. Griffiths and Heemstra (1995) identified three species, *A. japonicus*, *A. thorpei* and *A. inodorus*, which have different distribution ranges along the southern African coast. The *Argyrosomus* larvae collected in the present study are most likely that of *A. japonicus,* because the species is often found inshore and in estuaries on the KwaZulu-Natal coast. *A. thorpei* is a more offshore species and usually does not enter estuaries, and *A. inodorus* is a cold-water species, generally found south of East London (Griffiths and Heemstra 1995). The only description of early life-history stages of kob in South Africa was done by Beckley (1990), who described *A. hololepidotus* larvae from Algoa Bay. Those larvae were probably what is now known as *A. inodorus*.

Begg (1978) listed four main impacts of the harbour development on Durban Bay: (1) elimination of marginal vegetation, (2) removal of suitable substrata as feeding grounds, (3) industrial pollution and (4) increased tidal exchange. The increased tidal exchange would influence most 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 off California indicated size of the opening of an embayment to the sea is 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 is estimated to be 13.5×10^6 m^3 (Forbes *et. al.* 1994). Richards Bay Harbour (190 km north of Durban Harbour) has a larger tidal volume of 25×10^6 m^3, with 72 % of all

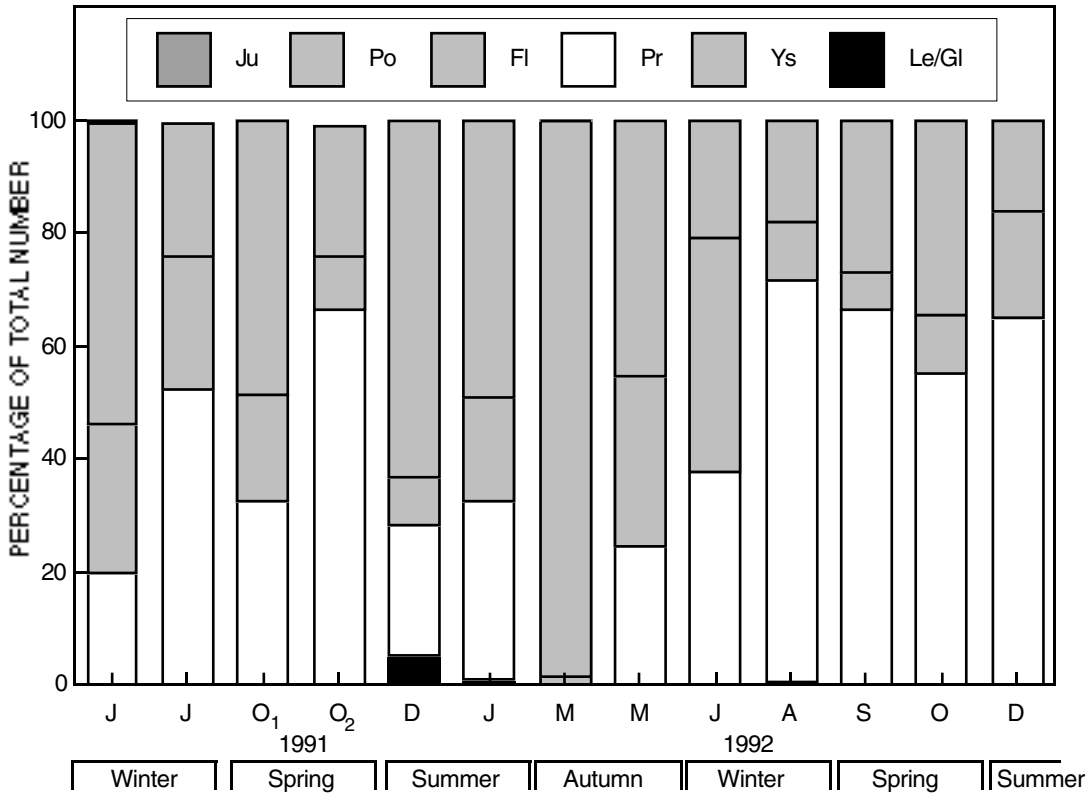

Fig. 8: Monthly percentage composition of developmental stages of all larvae sampled during the study (Le/Gl = leptocephalus/glass eel, Ys = yolk sac, Pr = preflexion, Fl = flexion, Po = postflexion, Ju = juvenile)

species being marine stragglers (Harris and Cyrus 1997). St Lucia Estuary has only 2×10^6 m^3 entering the system, with 44% of the species being larvae of marine stragglers (Harris and Cyrus 1995). By comparison, the Durban Harbour marine straggler assemblage constitutes 81% of all species. Whangateau Harbour, in northern New Zealand, is a small (9.2 km^2), bar-built estuary with extensive tidal flushing, and therefore having essentially marine conditions (Roper 1986) and a composition of fish larvae similar to the 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 they attributed to the restricted tidal exchange through the narrow and shallow entrance channel of that system.

Another reason to explain the dominance of marine-spawned larvae found in the present study is that sampling took place mostly in the lower reaches of Durban Harbour. Neira *et al.* (1992) found that most larvae caught in the lower reaches of the Swan Estuary, South-Western Australia, belonged to marine species, whereas those in the upper estuary almost exclusively represented estuarine spawner species.

Recruitment of marine species into Durban Harbour

Are the dominant marine species in Durban Harbour recruiting at the larval developmental 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. However, their sampling of larval stages was not adequate. Of the 144 larval species collected during the present study, 27 have been recorded as juveniles and/or adults in Durban Harbour (Table II). Of those species, 21 (78%) are species that are dependent or

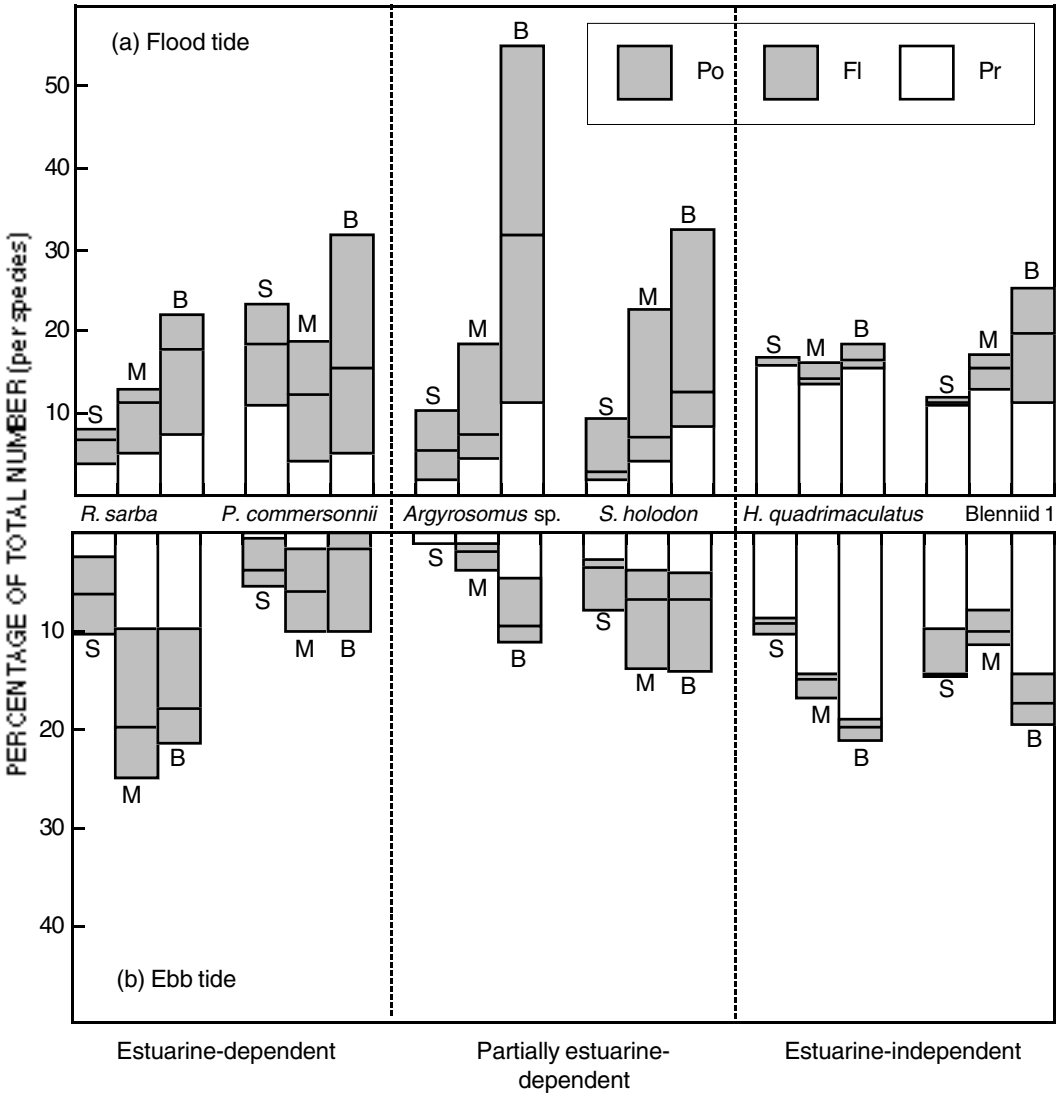

Fig. 9: Percentage composition of developmental stages for the most abundant species in each estuarine-association category on (a) flood and (b) ebb tides for the study period (S = surface, M = middle, B = bottom)

partially dependent on estuaries and were collected as larval stages in the present study, e.g. *R. sarba* and *P. commersonnii.* This suggests that certain estuarine-associated species utilizing Durban Harbour as a nursery area are recruiting into the system as larvae. There is evidence of inshore spawning by *P. commersonnii* and *R. sarba* (Wallace 1975b), which may explain the abundance of their larval stages within Durban Harbour. Similarly, in Richards Bay Harbour, a high percentage (84%) of the estuarine-associated fish species recorded as juveniles and/or adults in the system were also recorded as larvae (Harris and Cyrus 1997). 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 species

in the present study) abundant as juveniles and/or adults (Neira and Potter 1992, 1994). These fish therefore are recruited into these estuaries (Nornalup-Walpole Estuary and Wilson Inlet) as juveniles or adults, rather than as larvae. Because the majority of marine straggler larvae were sampled on both flood and ebb tides (Table II, Appendix), it would appear that the majority of those larvae that enter the Durban estuarine system on flood tides get swept out of the bay on the ebb tide.

Larval fish abundance in relation to environmental factors

In its natural state, Durban Bay was more estuarine in character, with a shifting sandbar situated at the entrance channel (Begg 1978). With the development of Durban Bay into a shipping port, the entrance channel was dredged and consequently increased the tidal exchange into the system substantially, resulting in the almost marine conditions which exist today. Day and Morgans (1956) found that the salinity, temperature and turbidity of the water in the bay resembled marine conditions, i.e. small ranges in environmental variables. This study and those of Hay *et al.* (1993), Beckley *et al.* (1994) and Graham (1994) have shown that these conditions still prevail, with high salinities ($>30 \times 10^{-3}$), temperatures that vary seasonally (18–27°C) and generally low turbidities (1–22 NTU). Such conditions are therefore suitable for marine and euryhaline estuarine fish.

In the present study, larval densities were significantly correlated to temperature, salinity and turbidity, accounting for 22% of the variation in larval densities of all species combined. However, this implies that more than 70% of this variation is unexplained. Similarly, in Richards Bay Harbour (Harris and Cyrus 1997) and the St Lucia Estuary (Harris and Cyrus 1995), temperatures, salinity and turbidity correlated significantly with larval densities and were species-specific. In Durban Harbour, abundances of dominant species peaked during autumn and winter when the water temperatures were lowest. Salinity and turbidity are important factors associated with larval and juvenile fish abundances (Cyrus and Blaber 1987a, b, Whitfield 1994a). However, Boehlert and Mundy (1988) suggested that it is a suite of factors associated with tidal flux at particular locations that acts as cues for recruiting fish larvae.

It is noteworthy that larvae of the dominant estuarine-independent species (e.g. *H. quadrimaculatus*) avoided highly turbid waters in Durban Harbour (Table III). Conversely, in the St Lucia Estuary, where estuarine-dependent species (e.g. *Glossogobius callidus* and *G. aestuaria*) dominated the catch, densities were significantly higher at higher turbidities (Harris and Cyrus 1995). Correlations between larval densities and environmental variables seem to be revealed only for the dominant species present in a particular system.

Temporal and spatial trends in larval fish abundance

Two important recreational and commercial linefish species on the KwaZulu-Natal coast are the dusky kob *A. japonicus* and the grunter *P. commersonnii* (Van der Elst 1981). *A. japonicus* spawn between winter and spring (Griffiths and Hecht 1993), with subsequent recruitment of juveniles (8–15 cm total length) into the estuarine environment (Wallace and Van der Elst 1975). The *Argyrosomus* sp. larvae in the present collections were relatively abundant in Durban Harbour during spring and early summer (Fig. 6). Their size range of 2.5–11.0 mm (mean 5.5 mm, see Table II) suggests that spawning takes place near the harbour mouth. Similarly, *P. commersonnii* is known to spawn in winter (Wallace and Van der Elst 1975, Van der Elst 1981), the period when their larval stages (size range 3.0–13.0 mm, mean 5.9 mm, Table II) were abundant in the harbour (Fig. 6).

There were different peaks in larval abundance 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 be more abundant in spring, summer and early autumn and less abundant in winter (Melville-Smith and Baird 1980, Whitfield 1989, Harrison and Whitfield 1990, Tzeng and Wang 1992, Neira and Potter 1994). Larval abundance of estuarine species in Durban Harbour appeared to peak at similar times. The peaks in winter were attributable to the presence of marine species such as *H. quadrimaculatus,* Blenniid 1 and *B. atlanticus.*

Although Durban Harbour is not a typical estuary, the abundance of estuarine-associated fish in the bay suggests that patterns of recruitment and maintenance of those species in the system are similar to those reported for typical estuarine environments. Whereas 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. The stage of development at which fish are present in inlets or estuaries may largely determine their ability to alter

their distribution (Boehlert and Mundy 1988). Recruitment and retention mechanisms in relatively deep estuaries that have a two-layered water column utilize tidal-stream transport (Weinstein *et al.* 1980, Fortier and Leggett 1983, Boehlert and Mundy 1988). In these systems, larval stages of estuarine fish 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, e.g. the goby *Rhombosolea plebia,* do settle on the bottom to avoid being swept out on ebb tides (Roper 1986). The entrance channel into Durban Harbour is about 13 m deep (129 m wide), so similar retention mechanisms and patterns of recruitment there may be expected.

In the present study, the tidal exchange of larvae into and out of Durban Harbour showed clear species-specific trends in abundance with respect to tide and depth. The larval densities of the dominant estuarine-associated species were highest on flood tides, suggesting a net input into the system (see Table IV). However, densities of these species were highest in middle and bottom waters (where currents are reduced) on both flood and ebb tides, indicating that the larvae were avoiding both tides. This pattern was particularly evident for the sciaenid *Argyrosomus* sp. (see Fig. 9), but because very few larvae (and only preflexion stages) were found in the surface samples on the ebb tide, there appears to be some degree of retention within the system as a result of selective tidal stream transport. In estuaries on the east coast of the USA, larvae of sciaenids (Atlantic croaker *Micropogonias undulatus* and weakfish *Cynoscion regalis*) have also been shown to be more abundant in middle and bottom depths on both flood and ebb tides, and to use selective tidal stream transport to effect retention in the estuary (Hettler and Barker 1993, Rowe and Epifanio 1994). However, the tidal pattern found by larvae moving in and out of a system can depend on the time and part of the tidal cycle sampled (Rijnsdorp and van Stralen 1985, Holt and Holt 1995). In other words, there are substantial daily differences in patterns of larval movement in out of an estuarine or harbour system. Future tidal exchange studies should take cognisance of this fact.

CONCLUSIONS

The impact of harbour development on the original estuarine system of "Port Natal" into the present day shipping port of Durban Harbour is clearly indicated by the composition of its larval fish assemblage. The presence of a permanently open, deep harbour entrance has resulted in increased tidal exchange of seawater, hence the dominance of marine species in the present study. The implication of this is that Durban Bay no longer functions as a "true estuarine" system. However the present sampling site was near the entrance channel of the harbour, in the lower reaches of the system, and it is likely that a more typical estuarine larval assemblage would be found in the middle and upper reaches of the estuarine system. Despite the semi-natural estuarine environment of Durban Harbour, the high species diversity of fish larvae in the system indicates that the harbour is in a relatively good ecological condition, as was shown for its juvenile and adult fish populations (Hay *et al.* 1995).

ACKNOWLEDGEMENTS

Drs J. M. Leis (Australian Museum, Sydney) and L. E. Beckley (Oceanographic Research Institute, Durban) are thanked for their help in the identification of larvae. Drs M-P. Olivar (Instituto de Ciencias del Mar, Barcelona) and A. D. Connell (CSIR, Durban) are acknowledged for the identification of larvae in the families Myctophidae and Sparidae respectively. Helpful criticism of the manuscript was provided by Dr Beckley. PORTNET is thanked for permission to work in Durban Harbour, as is SASOL, who sponsored the research boat used on the project and funded the research assistant post filled by SAH. This paper forms part of the Estuaries Special Programme (Natal Section), funded as a joint venture through the Foundation for Research Development, with additional funding provided by the University of Zululand Research Committee.

LITERATURE CITED

ABLE, K. W. 1978 — Ichthyoplankton of the St. Lawrence Estuary: composition, distribution, and abundance. *J. Fish. Res. Bd Can.* **35**(12): 1518–1531.

BEGG, G. [W.] 1978 — The estuaries of Natal. *Natal Tn reg. Plann. Rep.* **41**: 657 pp.

BECKLEY, L. E., VAN DER ELST, R. P., CHATER, S. A. and S. L. BIRNIE 1994 — Trapping of fishes in the Durban Harbour graving dock. Unpublished Report, Oceanographic Research Institute, South Africa **97**: 11 pp.

BECKLEY, L. E. 1990 — A description of the early life history stages of the kob, *Argyrosomus hololepidotus* (Pisces: Sciaenidae), from South Africa. *S. Afr. J. Zool.* **25**(4): 224–228.

BLABER, S. J. M., BREWER, D. T. and J. P. SALINI 1989 —

Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. *Estuar. coast. Shelf Sci*. **29**: 509–531.

BOEHLERT, G. W. and B. C. MUNDY 1988 — Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. In *Larval Fish and Shellfish Transport through Inlets*. Weinstein, M. P. (Ed.). *Am. Fish. Soc. Symp*. **3**: 51–67.

CYRUS, D. P. and S. J. M. BLABER 1987a — The influence of turbidity on juvenile marine fishes in estuaries. 1. Field studies at Lake St. Lucia on the southeastern coast of Africa. *J. expl mar. Biol. Ecol*. **109**: 53–70.

CYRUS, D. P. and S. J. M. BLABER 1987b — The influence of turbidity on juvenile marine fish in the estuaries of Natal, South Africa. *Continent. Shelf Res*. **7**(11/12): 1411–1416.

CYRUS, D. P. and A. T. FORBES 1994 — The role of harbours in Natal, South Africa, as alternative nursery sites for juvenile marine fish normally utilizing estuaries. In *Proceedings of the 4th Indo-Pacific Fish Conference*, *Bangkok*, *Thailand, November–December 1993*: p. 340.

CYRUS, D. P. and A. T. FORBES 1996 — Preliminary results on the role of KwaZulu-Natal harbours as nursery grounds for juveniles of selected marine organisms which utilize estuaries. *S. Afr. J. Wildl. Res*. **26**: 26–33.

DAY, J. H. and J. F. C. MORGANS 1956 — The ecology of South African estuaries. 7. The biology of Durban Bay. *Ann. Natal Mus.* **13**(3): 259–312 + 1 Plate.

FAHAY, M. P. 1983 — Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. *J. NW. Atl. Fish. Sci.* **4**: 423 pp.

FORBES, A. T., NIEDINGER, S. and N. T. DEMETRIADES 1994 — Recruitment and utilization of nursery grounds by penaeid prawn postlarvae in Natal, South Africa. In *Changes in Fluxes in Estuaries: Implications from Science to Management*. Dyer, K. R. and R. J. Orth (Eds). Fredensborg; Olsen & Olsen: 379–384.

FORTIER, L. and W. C. LEGGETT 1983 — Vertical migrations and transport of larval fish in a partially mixed estuary. *Can. J. Fish. aquat. Sci*. **40**:1543–1555.

GAUGHAN, D. J., NEIRA, F. J., BECKLEY, L. E. and I. C. POTTER 1990 — Composition, seasonality and distribution of the ichthyoplankton in the Lower Swan Estuary, south-western Australia. *Aust. J. mar. Freshwat. Res*. **41**: 529–543.

GRAHAM, M. A. 1994 — Association of juveniles of four fish species with sandbanks in Durban Bay, KwaZulu-Natal. M.Sc. thesis, University of Natal: 108 pp.

GRIFFITHS, M. H. and T. HECHT 1993 — Two South African *Argyrosomus hololepidotus* species: implications for management. In *Fish, Fishers and Fisheries. Proceedings of the Second South African Marine Linefish Symposium, Durban, October 1992*. Beckley, L. E. and R. P. van der Elst (Eds). *Spec. Publ. oceanogr. Res. Inst. S. Afr*. **2**: 19–22.

GRIFFITHS, M. H. and P. C. HEEMSTRA 1995 — A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Sciaenidae), with descriptions of two new species from southern Africa. *Ichthyol. Bull. J. L. B. Smith Inst. Ichthyol*. **65**: 40 pp.

GUASTELLA, L. A-M. 1994 — A quantitative assessment of recreational angling in Durban Harbour, South Africa. *S. Afr. J. mar. Sci*. **14**: 187–203.

HARRIS, S. A. and D. P. CYRUS 1995 — Occurrence of fish larvae in the St Lucia Estuary, KwaZulu-Natal, South Africa. *S. Afr. J. mar. Sci.* **16**: 333–350.

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

HARRIS, S. A. and D. P. CYRUS 1997 — Composition, abundance and seasonality of larval fish in Richards Bay harbour, KwaZulu-Natal, South Africa. *S. Afr. J. aquat. Sci.* **23**(1): 56–78.

HARRIS, S. A., CYRUS, D. P. and A. T. FORBES 1995 — The larval fish assemblage at the mouth of the Kosi Estuary, KwaZulu-Natal, South Africa. *S. Afr. J. mar. Sci*. **16**: 351–364.

HARRISON, T. D. and A. K. WHITFIELD 1990 — Composition, distribution and abundance of ichthyoplankton in the Sundays River estuary. *S. Afr. J. Zool*. **25**(3): 161–168.

HAY, D. G., BREEN, C., FORBES, T. and D. P. CYRUS 1993 — The development of a conceptual basis for the environmental management of the Port of Durban. *Investl Rep. Inst. nat. Resour. S. Afr*. **78**: 39 pp.

HAY, D. G., FORBES, A. T. and D. P. CYRUS 1995 — The biological status of the Ports of Natal and their role as alternative nursery grounds for juveniles of marine organisms normally occurring in estuaries. In *Disturbance and Evolution as Factors Influencing the Structure and Functioning of Estuaries*. Hay, D. G. and C. M. Breen (Eds). *Investl Rep. Inst. nat. Resour. S. Afr*. **107**: 80–96.

HETTLER, W. F. and D. L. BARKER 1993 — Distribution and abundance of larval fishes at two North Carolina inlets. *Estuar. coast. Shelf Sci.* **37**: 161–179.

HOLDEN, W. C 1855 — *History of the Colony of Natal*. South Africa; African Publishers.

HOLT, S. A. and G. J. HOLT 1995 — Temporal variability of ichthyoplankton in a tidal inlet in relation to physical processes. *Abstracts of the International Larval Fish Conference, Sydney, June 1995*: p. 57.

HORN, M. H. and L. G. ALLEN 1976 — Numbers of species and faunal resemblance of marine fishes in California bays and estuaries. *Bull. south Calif. Acad. Sci.* **75**(2): 159–169.

KENDALL, A. W., AHLSTROM, E. H, and H. G. MOSER 1984 — Early life history stages of fishes and their characters. In *Ontogeny and Systematics of Fishes*. Moser, H. G., Richards, W. J., Cohen, D. M., Fahay, M. P., Kendall, A. W. and S. L. Richardson (Eds). *Spec. Publ. Am. Soc. Ichthyol. Herpetol*. **1**: 11–22 (Proceedings of an International Symposium in La Jolla, California, August 1983).

LEIS, J. M. 1991 — The pelagic stage of reef fishes: the larval biology of coral reef fishes. In *The Ecology of Fishes on Coral Reefs*. Sale, P. F. (Ed.). San Diego; Academic Press: 183–230.

LEIS, J. M. and D. S. RENNIS 1983 — The Larvae of Indo-Pacific Coral Reef Fishes. Honolulu; University of Hawaii Press: 269 pp.

LEIS, J. M. and T. TRNSKI 1989 — The Larvae of Indo-Pacific Shorefishes. Honolulu; University of Hawaii Press: 371 pp.

MELVILLE-SMITH, R. and D. BAIRD 1980 — Abundance, distribution and species composition of fish larvae in the Swartkops Estuary. *S. Afr. J. Zool.* **15**(2): 72–78.

MOSER, H. G., RICHARDS, W. J., COHEN, D. M., FAHAY, M. P., KENDALL, A. W. and S. L. RICHARDSON (Eds) 1984 — *Ontogeny and Systematics of Fishes. Spec. Publ. Am. Soc. Ichthyol. Herpetol*. **1**: 760 pp. (Proceedings of an International Symposium in La Jolla, California, August 1983).

NEIRA, F. J. and I. C. POTTER 1992 — The ichthyoplankton of a seasonally closed estuary in temperate Australia. Does an extended period of opening influence species composition? *J. Fish Biol*. **41**(6): 935–953.

NEIRA, F. J. and I. C. POTTER 1994 — The larval fish assemblage of the Nornalup-Walpole Estuary, a permanently open estuary on the southern coast of western Australia.

Aust. J. mar. Freshwat. Res. **45**(7): 1193–1207.
NEIRA, F. J., POTTER, I. C. and J. S. BRADLEY 1992 — Seasonal and spatial changes in the larval fish fauna within a large temperate Australian estuary. *Mar. Biol*. **112**(1): 1–16.
OKIYAMA, M. 1988 — *An Atlas of the Early Stage Fishes in Japan*. Tokyo; Tokai University Press: 1154 pp.
RIJNSDORP, A. D. and M. VAN STRALEN 1985 — Selective tidal transport of North Sea plaice larvae *Pleuronectes platessa* in coastal nursery areas. *Trans. Am. Fish. Soc*. **114**: 461–470.
ROPER, D. S. 1986 — Occurrence and recruitment of fish larvae in a northern New Zealand estuary. *Estuar. coast. Shelf Sci.* **22**: 705–717.
ROWE, P. M. and C. E. EPIFANIO 1994 — Tidal stream transport of weakfish larvae in Delaware Bay, USA. *Mar. Ecol. Prog. Ser.* **110**: 105–114.
SMITH, M. M. and P. C. HEEMSTRA (Eds) 1986 — *Smiths' Sea Fishes*. Johannesburg; Macmillan: xx + 1047 pp.
TZENG, W-N. and Y-T. WANG 1992 — Structure, composition and seasonal dynamics of the larval and juvenile fish community in the mangrove estuary of Tanshui River, Taiwan. *Mar. Biol*. **113**(3): 481–490.
VAN DER ELST, R. P. 1981 — A Guide to the Common Sea Fishes of Southern Africa. Cape Town; Struik: 367 pp.
WALLACE, J. H. 1975a — The estuarine fishes of the east coast of South Africa. 1. Species composition and length distribution in the estuarine and marine environments. 2. Seasonal abundance and migrations. *Investl Rep. oceanogr. Res. Inst. S. Afr.* **40**: 72 pp.
WALLACE, J. H. 1975b — The estuarine fishes of the east coast of South Africa. 3. Reproduction. *Investl Rep. oceanogr. Res. Inst. S. Afr*. **41**: 51 pp.
WALLACE, J. H. and R. P. VAN DER ELST 1975 — The estuarine fishes of the east coast of South Africa. 4. Occurrence of juveniles in estuaries. 5. Ecology, estuarine dependence and status. *Investl Rep. oceanogr. Res. Inst. S. Afr.* **42**: 63 pp.
WEINSTEIN, M. P., WEISS, S. L., HODSON, R. G. and L. R. GERRY 1980 — Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. *Fishery Bull., Wash*. **78**(2): 419–436.
WHITFIELD, A. K. 1989 — Fish larval composition, abundance and seasonality in a southern African estuarine lake. *S. Afr. J. Zool*. **24**(3): 217–224.
WHITFIELD, A. K. 1994a — An estuary-association classification for the fishes of southern Africa. *S. Afr. J. Sci*. **90**(7): 411–417.
WHITFIELD, A. K. 1994b — Abundance of larval and 0+ juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. *Mar. Ecol. Prog. Ser*. **105**(3): 257–267.

APPENDIX

Taxa contributing <3% of the total catch of all estuarine-independent fish larvae collected at the study site in Durban Harbour

Species	Total catch			Body length (mm)		Developmental stages	Presence	Juvenile and adult present[A]
	Number	Mean density (·100 m^3)	% of total catch	Mean	Range			
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	
Mugulid 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	
Apistus 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 sexfasciatus	3	0.01	<0.1	12.8	4.5–29.0	Po,Ju	F,E	
Ophichthys sp.2	3	0.01	<0.1	17	9.0–30.0	Le	F	
Apodocreedia vanderhorsti	1	0.01	<0.1	14		Po	F	
Tripterygiid 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	
Diagramma pictus	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 ditchela	1	0.01	<0.1	10		Pr	F	
Blenniid 8	1	0.01	<0.1	4.5		Pr	F	
Callogobius sp.	1	0.01	<0.1	5.5		Fl	F	

(Continued)

App. (*continued*)

Species	Total catch			Body length (mm)		Developmental stages	Presence	Juvenile and adult present[A]
	Number	mean density (·100 m^3)	% of total catch	Mean	Range			
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	+
Mugilid 1	1	<0.01	<0.1	5		Fl	F	
Gempylid 2	1	<0.01	<0.1	22		Pr	F	
Muraenesox 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	
Lampanyctus 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)
Le = leptocephalus; Ys = yolk sac; Pr = preflexion; Fl = flexion; Jv = juvenile; F= flood tide; E = ebb tide
* Abundant
** Very abundant