A preliminary ichthyoplankton survey of the Tsitsikamma National Park

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An ichthyoplankton survey using bongo nets was conducted within the Tsitsikamma National Park over an 18-month period between January 1991 and July 1992. Four sampling stations along the coast were chosen, approximately 5 km apart. At each station four samples were taken along a transect perpendicular to the coast, between 0,35 km and 3,8 km offshore. Horizontal tows were taken at three and 15 m below the surface over reef and sand substrata respectively. Larvae belonging to 24 of the 35 families and 55 of the 97 species known to occur in the area were captured. Engraulid larvae completely dominated the catches while amongst the reef-associated taxa sparids and blenniids were prominent. Seasonally occurring cold upwelling events impacted negatively on egg and larval abundance. Mean values for egg and larval abundances were 1207 and 282 per 100 m^3 respectively. A relationship between larval number and plankton volume was revealed. Most larvae captured were between 2,0 and 20,3 mm (SL), and in the preflexion condition. The absence of larger size classes in samples was attributed to net avoidance.

'n Igtioplankton-opname is oor 'n tydperk van 18 maande, tussen Januarie 1991 en Julie 1992 binne die Tsitsikamma Nasionale Park (TNP) gedoen met die gebruik van bongo-nette. Vier stasies is langs die kus gekies, ongeveer 5 km uitmekaar. By elke stasie is vier monsters op n lyn loodreg met die kus tussen 0,35 km en 3,8 km vanaf die strand geneem. Die nette is horisontaal getreil drie en 15 m onder die oppervlak en monsters is onderskeidelik oor sand en rif geneem. Larwes van 24 uit die 35 families en van 55 uit die 97 spesies wat in die TNP voorkom is gevang. Die familie Engraulidae het die vangste oorheers terwyl die Sparidae en Blenniidae prominent was onder die rifverwante visse. Seisoenale koue opwellings het 'n negatiewe uitwerking gehad op die hoeveelheid eiers en larwes. Gemiddelde waardes vir onderskeidelik eier- en larfhoeveelhede was 1207 en 282 per 100 m^3. 'n Verwantskap tussen die larfhoeveelhede en planktonvolume is opgemerk. Die meeste van die larwes in die monsters was tussen 2,0 en 20,3 mm lank (SL) en in die voorverbuigingsvorm. Die afwesigheid van die groter klasgroottes is aan netontduiking toegeskryf.

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Ichthyoplankton surveys in South African waters were pioneered by Gilchrist (1916) who reported on the eggs and larvae of several Cape fishes. Little ichthyoplankton survey work was published between then and the 1970s, when there was a resurgence in ichthyoplankton research, the bulk of which occurred in estuaries (Melville-Smith 1978, 1981; Melville-Smith & Baird 1980; Melville-Smith, Baird & Wooldridge 1981; Neira, Beckley & Whitfield 1988; Whitfield 1985, 1989a,b; Beckley 1984). In the marine environment Shelton & Kriel (1980) investigated the distribution of pelagic fish eggs and larvae off the south-east coast, Whitfield (1989c) worked in the surf zone and Beckley (1986) sampled the nearshore region immediately behind the breaker line and has also conducted an extensive ichthyoplankton survey on the east coast both on and beyond the continental shelf (Beckley & van Ballegooyen 1992; Beckley 1993). West coast ichthyoplankton research tended to concentrate on species important in the purse-seine fishery off the Namibian coast (South West Africa) in the 1970s (e.g. O'Toole 1977, 1978; Badenhorst & Boyd 1980; Boyd & Badenhorst 1981). Extensive offshore egg and larval surveys have also been conducted on the south coast (Shelton & Hutchings 1982; Hampton, Armstrong, Jolly & Shelton 1990; Boyd, Taunton-Clarke & Oberholster 1992). The present survey concentrated on the inshore zone between 0,35 km and 3,8 km offshore (20–80 m depth contours) within the Tsitsikamma National Park (TNP) on the south-east coast of South Africa. Ichthyoplankton composition, seasonality and abundance were investigated

and the study serves as a foundation for further work into the larval ecology of economically significant species, particularly regarding the nature and extent of their dispersal (Tilney, Buxton, Nelson & Radloff, in prep.). This study forms part of a larger programme to evaluate the role of the TNP, and by implication other marine reserves, in the management of South African linefish resources. The ability of marine reserves to sustain large, reproductively active core populations, and the extent to which they are exporters of recruits to adjacent, fished areas are the focus of this investigation.

Materials and Methods

Plankton samples were taken during daylight hours from the National Parks Board patrol vessel *Natpark Aonyx*, using 56 cm diameter bongo nets fitted with 500 μm mesh. Sample site selection was influenced by substratum type with two sites being over areas of high profile reef (Knoll and Rheeders) and two over sand (Sanddrif and Elands), (Figure 1). Samples were taken along four transects running perpendicular to the shoreline. The alongshore distance between transects was approximately 5 km. Three near-surface plankton hauls, between 1 m and 3 m deep, were taken along each transect at the 20, 40 and 80 m depth contours, approximately 0,35 km, 1,3 km and 3,8 km offshore respectively (Figure 1). At the 20-m station a second, deep horizontal haul was also taken, with the nets at a depth of approximately 15 m. The bongo frame was weighted and
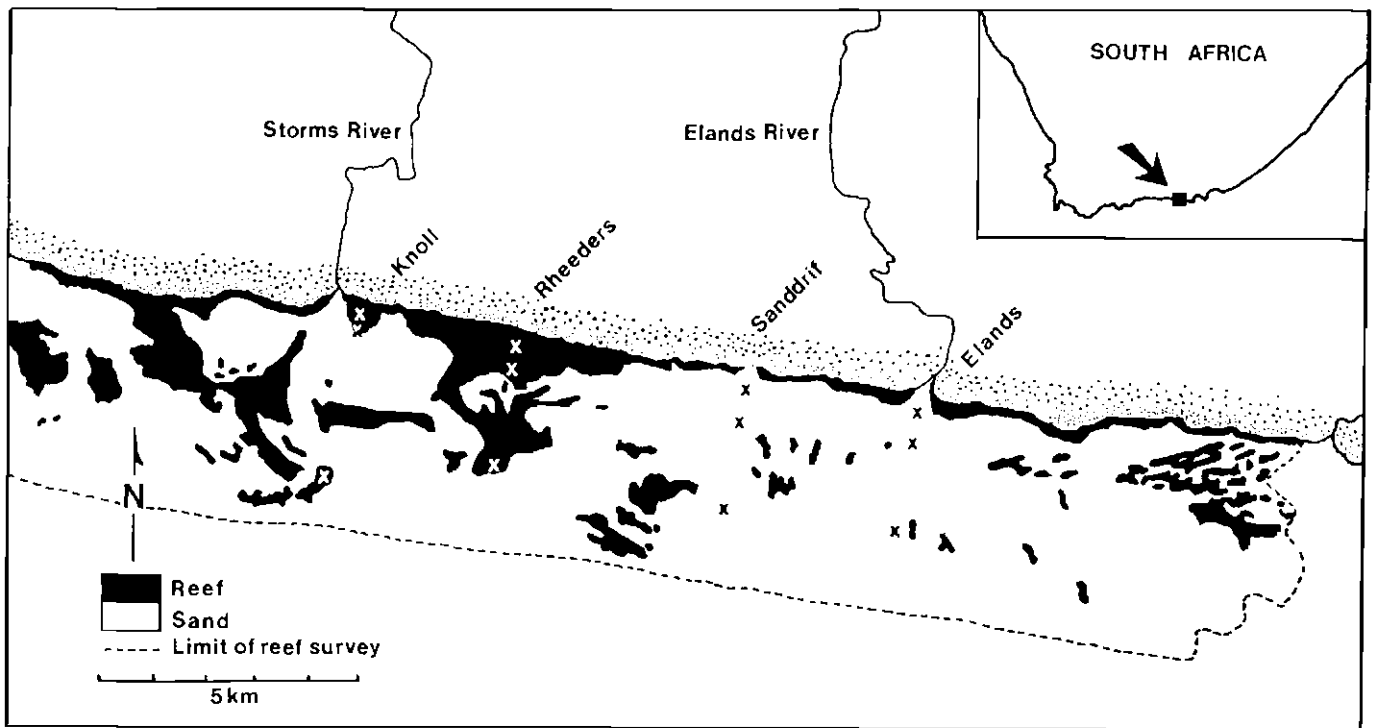
Figure 1 Part of the Tsitsikamma National Park showing the reef substratum and sampling sites at the Knoll, Rheeders, Sanddrif and Elands. Sampling stations marked by Xs (modified after Buxton 1987).

deployment depth was controlled by the length of the tow rope, which was 20 m long for the near-surface hauls and 80 m long for the deep hauls. Maximum deployment depth was controlled using a buoy tethered to the bongo frame, 5 m long for the near-surface hauls and 20 m long for the deep hauls. The nets were towed parallel to the shore into the wind, at a speed of approximately 1 m s^{-1} (2 knots) for 7 min. A calibrated General Oceanics digital flowmeter was mounted in the mouth of one of the nets, and each haul represented a filtered water volume of approximately 100 m^3. After retrieval the nets were washed down with a hand-operated bilge-type pump and the samples preserved in a 5% solution of formalin in sea water. In the laboratory plankton settled volumes were determined before the fish eggs and larvae were removed. Samples were sorted under a binocular microscope. Larvae were counted and identified to the lowest possible taxonomic level using texts by Moser *et al.* (1984), Brownell (1979), Leis & Rennis (1983), Leis & Trnski (1989) and Olivar & Fortuño (1991). Larvae were measured for standard length using an eyepiece micrometer to one tenth of a millimetre. The total number of eggs in each sample was recorded. Sea surface temperatures were measured during each plankton haul using a standard mercury thermometer, and monthly mean sub-surface (12 m depth) sea temperature data for the Storms River area was obtained from the Sea Fisheries Research Institute (J. Taunton-Clarke, pers. comm.). The study was conducted between January 1991 and July 1992 with sampling occurring monthly, weather permitting.

Results

A total of 13 434 larvae and 62 446 eggs were collected in 14 monthly samples. Larvae from 24 families were identi-

fied (Table 1). A small percentage of larvae (0,8%; n = 105) could not be identified to family level. The bulk of the larvae were in the post-yolksac, pre-flexion stage of development, probably attributable to the relatively large mesh size used (500 μm) in the first instance, and to net avoidance by larger larvae in the second instance.

Catch composition

The ichthyoplankton could be broadly separated into larvae from pelagic, reef- and sand-associated families, with some exceptions. Sparids incorporated both reef- and sand-associated species and the sciaenids both sand-associated and pelagic species. In terms of overall larval numbers the pelagic component was by far the most abundant, comprising approximately 77% of the total catch. Reef-associated families contributed 21% and sand-associated families the remaining 2% (Figure 2a). In terms of numbers of taxa, the reef component dominated with an estimated 31 species, followed by the sand (± 18 species) and pelagic (± seven species) habitats. Only a few larvae were identified to genus and/or species level, and all species identifications should be viewed as tentative in the light of the unavailability of complete size ranges for this purpose.

The pelagic component was made up of primarily clupeiform larvae, the bulk of which were engraulids (*Engraulis capensis* and possibly *Stolephorus holodon*). The small sizes of engraulids in samples precluded definitive identification. No engraulid eggs were encountered. The clupeids, *Sardinops sagax* and *Etrumeus* spp. were also abundant. A few carangid larvae identified as *Trachurus trachurus* and a single sciaenid, identified as *Atractoscion aequidens*, were also present (Figure 2b).

Sand-associated larvae were represented by 12 families

Table 1 Numbers, size ranges and taxa of fish larvae sampled in the TNP between January 1991 and July 1992
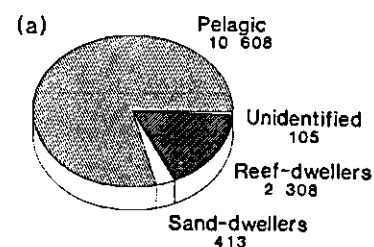
Taxon	n	No. of species	Size range SL (mm)
Order Clupeiformes			
Clupeidae	548	2–3	3,3–20,3
Engraulidae	10027	1–2	2,5–12,8
Order Gadiformes			
Gadidae	57	1	2,5–5,7
Order Gobiesociformes			
Gobiesocidae	416	2	2,7–9,2
Order Syngnathiformes			
Syngnathidae	8	1	15,0–36,0
Order Scorpaeniformes			
Tetrarogidae	45	1	2,2–5,3
Congiopodidae	1	1	3,8
Triglidae	1	1	10,0
Order Perciformes			
Serranidae	1	1	5,5
Haemulidae	88	1	1,8–12,3
Sparidae	846	17	2,0–12,8
Monodactylidae	1	1	5,0
Sciaenidae	15	3	2,2–7,7
Carangidae	32	1	2,9–6,2
Cheilodactylidae	74	2	2,7–4,7
Mugilidae	1	1	4,0–4,7
Blenniidae	772	3	2,5–19,0
Clinidae	191	3	4,7–16,3
Ammodytidae	16	1	4,5–8,1
Callionymidae	2	1	2,5–6,5
Gobiidae	37	3	2,6–8,3
Order Pleuronectiformes			
Cynoglossidae	72	2	3,1–7,1
Soleidae	75	3	2,7–5,6
Order Tetraodontiformes			
Tetraodontidae	3	1	2,0–3,1
Unidentified	105	–	1,2–3,5

TOTAL NUMBERS

N • 10 608

N • 413

N • 2 307

Figure 2 (a) Total ichthyoplankton catch composition sampled in the TNP between January 1991 and July 1992, taxa split according to adult habitat type, (b) the pelagic, (c) sand-associated and (d) reef-associated ichthyoplankton fractions.

including Ammodytidae, Callionymidae, Cynoglossidae (*Cynoglossus* spp.), Gobiidae (*Caffrogobius* spp.), Haemulidae (*Pomadasys olivaceum*), Mugilidae, Sciaenidae (*Argyrosomus* sp. and *Umbrina* sp.), Soleidae (*Heteromycteris capensis* and *Solea bleekeri*), Sparidae (*Pagellus belottii natalensis*), Syngnathidae (*Syngnathus acus*), Tetraodontidae (*Amblyrhynchotes honckenii*) and Triglidae (*Chelidonichthys kumu*) (Figure 2c).
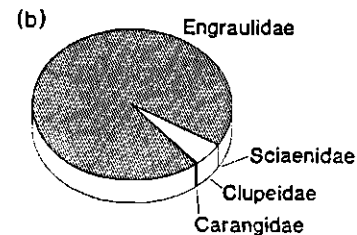
The reef-associated component was represented by larvae from eight families including Blenniidae (*Parablennius* spp.), Clinidae (*Pavoclinus* sp.), Congiopodidae (*Congiopodus spinifer*), Monodactylidae (*Monodactylus falciformis*), Gadidae (*Gaidropsarus capensis*), Gobiesocidae (*Apletodon pellegrini*), Tetrarogidae (*Coccotropsis gymnoderma*) and Sparidae (*Spondyliosoma emarginatum*) (Figure 2d).
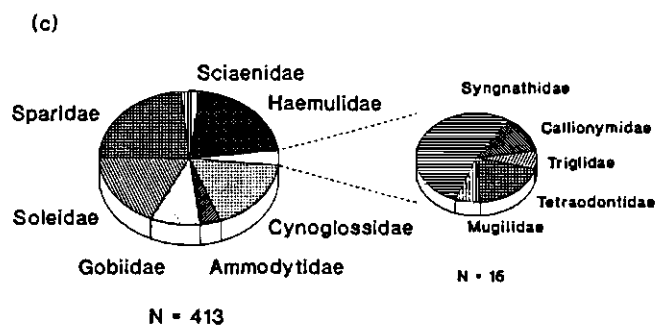
Annual sea temperature regime

The monthly instantaneous sea surface temperatures (Table 2) demonstrate the wide fluctuation in temperatures that occurred during the sampling programme. The mean subsurface sea temperature for the autumn/winter period
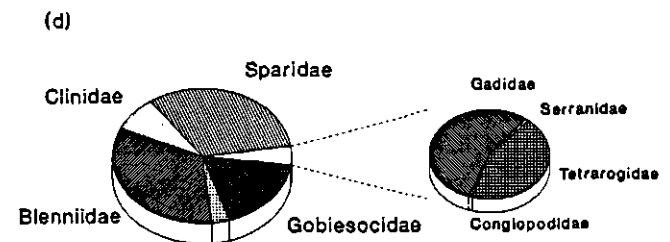
(March – August) was only 3°C colder than that of the spring/summer period (September – February). Temperature ranges were far greater during spring/summer owing to the occurrence of cold upwelling events at this time of year (Figure 3).

Egg and larval seasonality

Eggs appeared to be most abundant during mid-summer and showed a general decline with the onset of autumn and winter, although the July 1992 sample yielded an uncharacteristically high egg catch (Figure 4). There was a very wide range between the upper (2895,8 per 100 m^3) and

Table 2 Mean monthly egg and larval numbers (per 100 m³) and instantaneous, monthly sea surface temperatures measured in the TNP between January 1991 and July 1992

	No. of eggs	(SD)	No. of larvae	(SD)	Instantaneous sea temp. (°C)
Jan '91	2014,8	(231,9)	2895,8	(803,5)	23,0
Feb '91	1762,5	(295,2)	162,0	(20,3)	21,6
Apr '91	1094,1	(132,5)	185,7	(30,8)	16,4
May '91	701,3	(110,6)	220,8	(22,3)	19,0
Jul '91	468,6	(43,8)	23,9	(3,6)	17,0
Sep '91	290,2	(29,4)	68,7	(8,2)	18,0
Oct '91	1294,5	(79,6)	100,7	(13,5)	15,2
Nov '91	1220,4	(131,4)	29,5	(3,2)	20,8
Dec '91	2821,7	(175,0)	93,9	(12,0)	20,1
Jan '92	1762,1	(243,6)	51,1	(8,6)	23,5
Feb '92	1012,9	(188,8)	14,4	(2,0)	15,8
Mar '92	522,4	(31,7)	4,3	(1,2)	19,7
Apr '92	408,6	(40,9)	11,1	(1,8)	19,4
Jul '92	1528,6	(100,1)	85,4	(6,2)	19,5

■ 20 m (Deep) ▨ 20 m (Surface) ⊞ 40 m (Surface) ◩ 80 m (Surface)

Figure 4 Total numbers (per 100 m³) of fish eggs sampled in the TNP between January 1991 and July 1992. 20 m (Deep) = sample taken over the 20-m contour with the net at 15 m depth; 20, 40 & 80 m (Shallow) = samples taken over 20, 40 & 80-m contours respectively with the net 3 m beneath the surface.
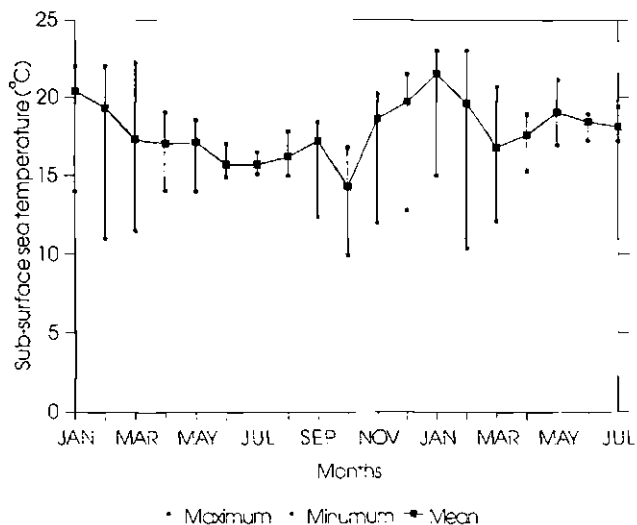

• Maximum • Minimum ─■─ Mean

Figure 3 Mean monthly sub-surface (12 m) sea temperatures and temperature ranges for the Storms River mouth area between January 1991 and July 1992.

■ 20 m (Deep) ▨ 20 m (Surface) ⊞ 40 m (Surface) ◩ 80 m (Surface)

Figure 5 Total numbers (per 100 m³) of fish larvae sampled in the TNP (a) between January 1991 and July 1992, and (b) between February 1991 and July 1992 (masking effect of high January 1991 catch removed).

lower (4,3 per 100 m³) extremes of mean monthly larval abundance, both of which occurred during the summer (Table 2). The very high engraulid catch (n = 8546) of January 1991 exceeded the total larval catch for the entire subsequent sampling programme (Figure 5a). Larval catches were erratic throughout the year (Figure 5b), and there was an absence of any marked seasonality.

Upwelling events appeared to impact negatively on larval abundance, as illustrated by the poor catches during February and March 1992 (Table 2; Figure 5b). The February sample was taken during, and the March sample shortly after, major upwelling episodes when temperatures dropped rapidly from 23 to 11°C and from 21 to 13°C respectively and yielded monthly mean larval numbers of 14,4 and 4,3 per 100 m³ against an overall mean of 282 per 100 m³ (or 80,9 per 100 m³ if the January 1991 anomaly
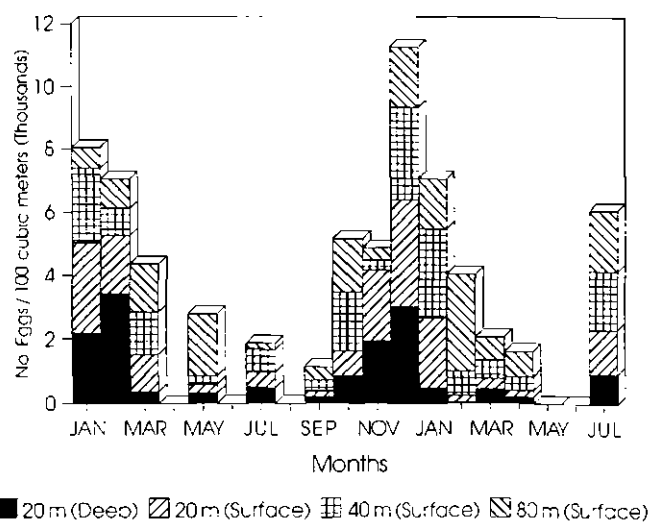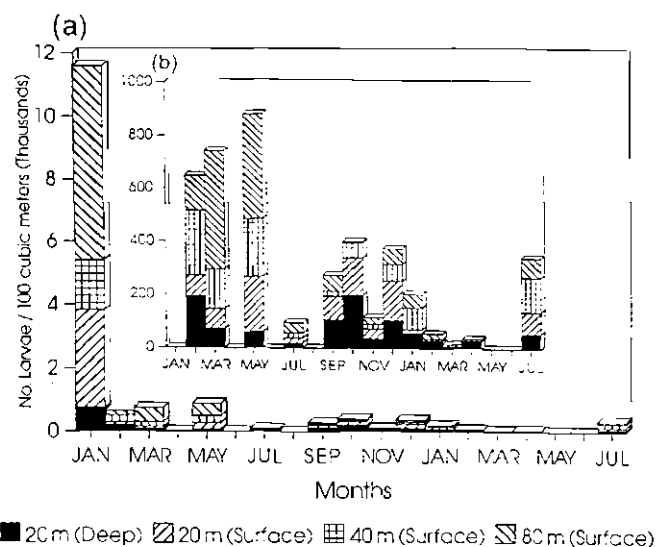
was discounted). There was, however, no statistically valid relationship between instantaneous monthly sea surface temperatures and egg (r^2 = 0,277) or larval (r^2 = 0,180) abundance, nor between mean monthly sea temperatures and egg (r^2 = 0,442) or larval (r^2 = 0,125) abundance. This was probably due to the fact that poor catches also occurred in the absence of upwelling events, e.g. during September 1991 and April 1992 for eggs, and during July 1991, November 1991 and April 1992 for larvae (Figures 4 & 5). To a large extent egg and larval catches were probably a function of their distributional patchiness. Egg numbers did not correlate well with larval numbers (r^2 = 0,276).

The relationship between plankton settled volume and egg

or larval numbers was also inconsistent ($r^2 = 0,002$ for eggs and $r^2 = 0,110$ for larvae). When the unusually large catch of engraulid larvae in January 1991 was excluded from the regression the larva – plankton relationship was vastly improved ($r^2 = 0,815$), suggesting a link between plankton abundance and larval survival.

Larvae from the dominant families were present in samples throughout the year suggesting that they incorporated both autumn/winter and spring/summer spawners. While clupeids, gadids and cheilodactylids appeared to be more abundant during autumn/winter, and engraulids and soleids more abundant during spring/summer, these differences were not significant (Figure 6).

Egg and larval distribution

The analyses of inter- and intra-station distribution are to be presented in detail elsewhere (Tilney *et al.* in prep.), and are only briefly referred to here. Statistical analyses were performed to test for differences in egg and larval abundance over reef vs. sand, inshore vs. offshore, and surface vs. deep samples. The total egg complement revealed a significantly higher occurrence over areas of sand than over areas of reef (Figure 7), an equal abundance at offshore (80 m) and inshore (20 and 40 m) stations, and a homogeneous distribution between surface (20 m shallow) and deep (20 m deep) samples (Figure 4). Analyses of the total larval complement revealed that they were homogeneously distributed with respect to reef vs. sand (Figure 8) and surface (20 m shallow) vs. depth (20 m deep), but that larval numbers at the offshore stations (80 m) were significantly higher than those at the inshore stations (20 and 40 m), (Figure 5). However, a considerable degree of masking occurred at this level of analysis where all taxa were treated as one. When they were performed independently for each larval family, quite distinct distributional behaviour patterns emerged (Tilney *et al.* in prep.), and it became evident that
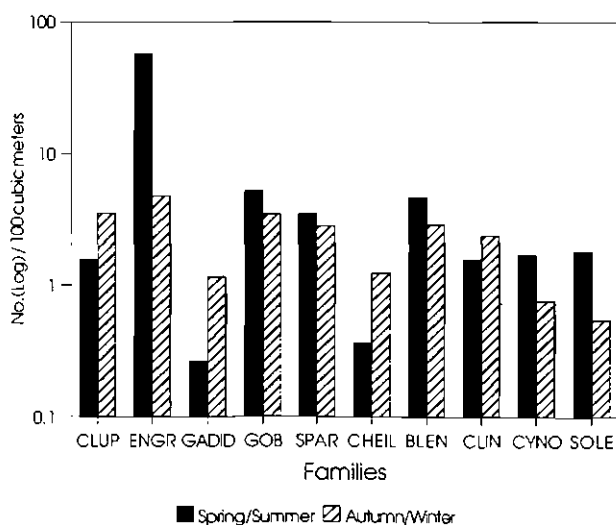

Figure 7 Comparison of egg catches (total numbers per 100 m³) taken over reef and sand substrata respectively, between January 1991 and July 1992.
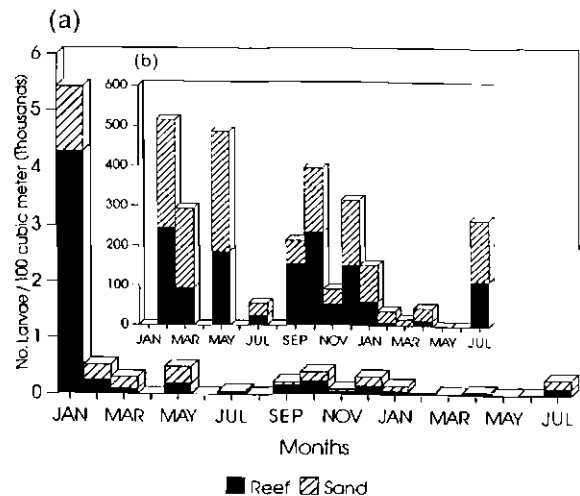
Figure 8 Comparison of larval catches (total numbers per 100 m³) taken over reef and sand substrata respectively, between (a) January 1991 and July 1992 and (b) between February 1991 and July 1992 (masking effect of high January 1991 catch removed).

larvae were capable of exercising a considerable degree of control over their distribution and dispersal.

Discussion

Beckley (1986) recognized three larval categories based on adult habits and reproductive behaviours, namely (i) pelagic taxa, (ii) coastal taxa producing benthic eggs or exhibiting viviparity, and (iii) coastal taxa producing pelagic eggs. In the present study 80% of the catch was from category (i) and 10% for each of categories (ii) and (iii). Engraulids dominated the samples numerically, comprising 75% of the total catch. Next most abundant were the sparids (6%) and blenniids (6%), clupeids (4%), gobiesocids (3%) and clinids (1%). Beckley (*op. cit.*), sampled the nearshore environment immediately behind the breaker line in Algoa Bay and found

Figure 6 Catch seasonality for the principal larval taxa sampled in the TNP between January 1991 and July 1992 (clup = Clupeidae; engr = Engraulidae; gadid = Gadidae; gob = Gobiesocidae; spar = Sparidae; cheil = Cheilodactylidae; blen = Blenniidae; clin = Clinidae; cyno = Cynoglossidae; sole = Soleidae).
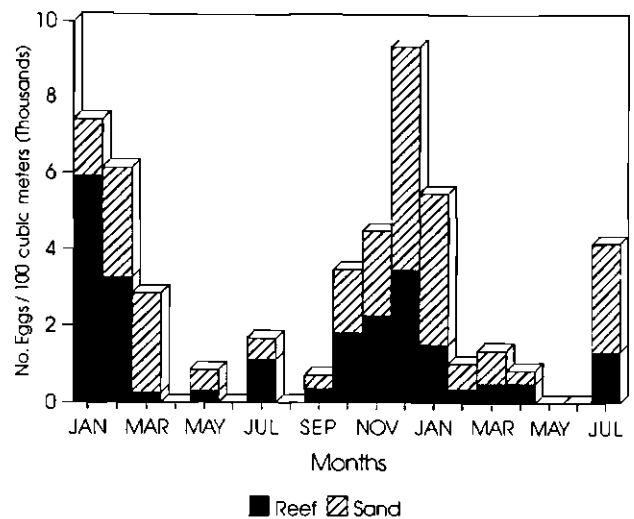
the most dominant taxa to be gobiidae (*Caffrogobius* spp.) although clupeids were also very abundant in this region. Interestingly, sparids in the above study were poorly represented and the author speculated that they spawned further offshore. This was confirmed by recent work in the Tsitsikamma (Tilney *et al.* in prep.) where it was found that sparid larvae were more abundant further out (3,8 km offshore) than they were closer inshore (between 0,35 km and 1,2 km offshore). Whitfield (1989c) found large size-class (8–22 mm) sparid larvae to be abundant within the breaker zone, indicating a complex larval distributional behaviour pattern within this family.

The taxonomic diversity in the ichthyoplankton samples from the present study was lower than expected with only 24 out of the 35 teleost families (excluding tropical migrants) found in the TNP (Burger 1990) being encountered. Representation at the species level was even poorer with only 55 resident teleost species being captured while 97 have been recorded in the TNP (Burger *op cit.*). Notable absentees from samples were the Serranidae of which only one larva was caught, and the Coracinidae and Oplegnathidae which were either misidentified or were completely absent. The poor cheilodactylid representation in samples was also surprising in the light of the abundance of three species of adults in the area. While it is recognized that cheilodactylids produce paper larvae with a protracted pelagic phase employing a more vast larval closure system (Vooren 1972), this does not explain the paucity of prepaper larva cheilodactylids caught.

The sparids with 17 species as against 22 listed by Buxton & Smale (1984) and 23 reported by Burger (1990), were well represented and were numerically the most abundant non-pelagic family, highlighting the role of the TNP as an important refuge area for reproductively active sparid populations.

The blenniids and gobiids were taxonomically well represented. Burger (1990), in an intensive inter- and subtidal rotenone sampling programme in the TNP found three gobiids (*Caffrogobius agulhensis, C. caffer* and *C. saldanha*) and three blenniids (*Chalaroderma ocellata, Parablennius cornutus* and *P. pilicornis*) and it seems that these species were all sampled in this study. While Burger (1990) found 19 clinid species in the TNP only three were sampled in this study, one of which was provisionally ascribed to the genus *Pavoclinus*. Their poor representation in the samples may be attributed to their style of reproduction. All southern African clinids are live bearers (Smith & Heemstra 1986) and young at parturition probably have a relatively short pelagic existence, or may recruit straight onto the reef, thereby being largely unavailable to plankton nets.

The two gobiesocids were probably *Apletodon pellegrini* and *Diplecogaster megalops*, the subtidally occurring species in the Tsitsikamma area (Buxton & Smale 1984; Burger 1990).

Two cynoglossids occur inshore along the south-east Cape coast (Smith & Heemstra 1986) and it is thought that both were present in the samples. The more abundant of the two was thought to be *Cynoglossis capensis* and the other, which occurred less frequently, *C. zanzibarensis*. Five soleid genera comprising six species occur in the area namely *Heteromycteris, Austroglossus, Synaptura, Synapturichthys*

and *Solea* (two species). The Cape sole, *Heteromycteris capensis* was fairly abundant in samples while a few *Synaptura* sp. larvae and a single *Solea bleekeri* larva were caught. Bothids were absent, as was the single pleuronectid *Paralichthodes algoensis* which occurs in the area (Smith & Heemstra *op. cit.*).

It was interesting that no engraulid eggs were encountered in samples and since both *Engraulis* and *Stolephorus*, the two engraulids likely to be encountered along the south-east coast have ovoid eggs (Leis & Trnski 1989), they are unlikely to have been missed during plankton sorting. Olivar & Fortuño (1991) report that anchovy eggs have a minimum diameter of 0,5 mm, which would have made it possible for some of them to have passed through the mesh. However, their total absence from samples would tend to suggest that they do not spawn inshore along the Tsitsikamma coast. Melville-Smith (1978) reported significant recruitment of *Stolephorus commersonii* (synonymous with *S. holodon*) larvae into the Swartkops estuary between January and March at the late larval and metamorphic stages. While the primary spawning ground for *Engraulis capensis* is between Cape Infanta and Cape Point (Shelton & Hutchings 1982), they are also thought to spawn in Algoa Bay (Beckley 1986), and along the shelf break off the south-east coast (Valdés, Shelton, Armstrong & Field 1987; Hutchings 1992). The engraulid larvae in the samples were too small to allow identification beyond family level and it is not presently known to which of the two genera they belonged.

The absence in samples of larvae from the larger size-classes proved to be a major stumbling block to identification, especially of the sparids which were of particular interest in the study. Gear avoidance by larvae is a problem not easily overcome by ichthyoplanktologists (e.g. Marcy & Dahlberg 1980; Gallagher & Conner 1983; Omori & Ikeda 1984; Munk 1988). Beckley (1986), who sampled at night using a very large plankton net (1,5 m diameter) also failed to capture large sparid individuals. Leis (1991) identified several characteristics of pelagic larvae which render them particularly difficult to sample adequately. These included rarity, distributional patchiness, temporal changes in spatial distribution patterns, the three-dimensional nature of their distribution and the fact that no single gear type is effective for capturing all ages (sizes), and taxa of larvae. The single sampling method employed in the present study was unsuited to the task of compiling developmental series of the larval taxa in the TNP. However, the study was designed primarily to investigate the distribution and dispersal of larvae (Tilney *et al.* in prep.) and the statistical analyses associated with this required that sampling variables be kept to a minimum. Additional work using a wider variety of capture techniques, including oblique hauls and diurnal sampling, will therefore be required to fill the size, and taxonomic, gaps evident from the results above.

The lack of seasonality in larval catches may have been caused by the unpredictability of the sampled environment and attributable to factors such as larval patchiness and the negative impact of upwelling events. Larval patchiness was evident from the high between-sample and between-month variability in catches. The large catch of engraulid larvae during January 1991 was probably the result of large scale inshore movement of these larvae under the influence of

persistent onshore or westerly wind conditions.

Upwelling events in the Tsitsikamma area were a regular phenomenon between September and March and have been well documented (Schumann, Perrins & Hunter 1982; Schumann, Ross & Goschen 1988). They occur when the establishment of a near-surface thermocline during the warmer months obstructs vertical water mixing and results in surface water warming. When easterly wind conditions prevail the warm, surface waters are moved offshore and are replaced inshore by cold, upwelled water. Rapid temperature declines often in excess of 10°C occur during these events and appear to impact negatively on inshore egg and larval numbers. It is not presently known whether the eggs and larvae are carried offshore by surface Ekman transport (Olivar 1990) or whether they succumb during upwelling events. The fact that some eggs and larvae were present inshore, albeit in fairly low numbers, during upwelling events would suggest that spawning continued unabated. However, an alternative explanation might be that these were spawned prior to upwelling events and had merely had their development arrested by the extreme cold. Either way, it would appear that upwellings have a major impact on inshore egg and larval aggregations either in the form of mortality owing to cold shock, or large scale offshore transport. Summer serial/repetitive spawners such as sparids (Thresher 1984; Buxton 1990) are in all probability able to absorb reproductive losses which may occur as a result of upwelling events, the effects of which typically dissipate over a period of several days (Schumann et al. 1982). Considering the frequency of upwelling events, and the long duration of the upwelling 'season' in the Tsitsikamma, it is more likely that larvae are well adapted to this phenomenon, and that upwelling events are manipulated to their best advantage. This has been demonstrated for several pelagic fish species in which spawning occurs in response to upwelling events (Checkley, Raman, Maillet & Mason 1988; Roy, Cury & Kifani 1992). While eggs and larvae are likely to be dispersed offshore during upwelling events it is also likely that these upwelling-induced currents are a part of the current closure system (sensu Sinclair 1988) employed by the pelagic stages of these inshore fishes. Eggs and larvae that are carried offshore during upwellings are likely to be transported in a westward direction in the coastal jet current that becomes established at the frontal zone between the warm and cold water bodies (E. Schumann, pers. comm.). Once the upwelling dissipates, they are likely to be transported back inshore some distance west of Tsitsikamma, under the influence of Stokes drift, which is generated by surface waves (E. Schumann, pers. comm.). Onshore transport may also occur following upwelling under westerly wind conditions when both onshore and easterly components would be introduced to the upper layers of the ocean. Eggs and larvae returning to the inshore environment would be able to capitalize on periods of high phytoplankton production which typically occur as a result of upwellings. While it is probable that nett losses of eggs and larvae occur from the Tsitsikamma region during upwelling events, these propagules are likely to be able to complete their life-cycle at some other point along the Cape south coast, further to the west. Similarly, the Tsitsikamma region may recruit larvae which originate from upwelling cells further to the east, e.g. Cape St Francis and

Cape Recife. It should be stressed, however, that the larvae of inshore fishes are not passively drifting particles whose distribution is dictated entirely by ocean currents (Leis & Goldman 1984; Marliave 1986; Leis 1991; Tilney et al. in prep.). Egg and larval distributional dynamics are complex and the impact that upwelling events have on survival, distribution and dispersal of reef fish larvae along the southeast coast warrants additional investigation.

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