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ICHTHYOPLANKTON DISTRIBUTION AND DISPERSAL IN THE TSITSIKAMMA NATIONAL PARK MARINE RESERVE, SOUTH AFRICA

The nature of ichthyoplankton distribution within the Tsitsikamma National Park marine reserve was investigated in an attempt to evaluate the potential for export of larvae of commercially and recreationally important reef species to adjacent, exploited areas. Monthly, inshore ichthyoplankton samples were taken using Bongo nets over an 18-month period. Sampling sites were located over areas of high-profile reef and sand. Current-meter measurements of the area were used to determine current velocity, direction and reversal periodicity. Statistical analysis of the data was performed independently for larvae from four families: Blenniidae, Gobiesocidae, Sparidae and Engraulidae. Results suggested that blenniid and gobiesocid larvae practised active position retention throughout their pelagic phase, while this feature was less defined in sparid and engraulid larval distribution. Using larval distribution and current-meter information, projected dispersal distances for sparid larvae, the family containing the most target commercial and recreational angling species, were estimated. The results suggest that sparid larvae are exported from the reserve to adjacent, exploited areas.

Marine reserves as a management option for inshore, and particularly reef-directed fisheries, offer several potential advantages over conventional strategies which regulate catch and effort. Among others are the conservation of biodiversity in an undisturbed reef community, increased public understanding and acceptance, simplified enforcement, research and educational opportunities and non-extractive recreational uses (Anon. 1990, Roberts and Polunin 1991). More directly, marine reserves are capable of protecting a spawner stock biomass that, in the absence of fishing mortality, has a natural population age structure (Roberts and Polunin 1991). Under such circumstances, potential fishery benefits are twofold: enhancement of catch in adjacent areas, through the movement of surplus individuals from the reserve, and a supply of recruits in fished areas by larval dispersal. Both processes are poorly understood. Bennett and Attwood (1991) provide evidence for the recovery of a surf-zone fishery following the establishment of a marine reserve on the Cape south coast, South Africa, but this has not been demonstrated elsewhere. Sub-adult and adult reef fish characteristically occupy fairly small home ranges (Bennett et al. 1989, Buxton and Allen 1989, Anon. 1990, Bennett and Attwood 1991) and consequently have low movement potential. The likelihood of pelagic phase (eggs and larvae) emigration is, however, far greater. The fate of the pelagic phases of neritic fish has been the focus of much attention (e.g. Norcross and Shaw 1984, Smith and Morse 1985, Cushing 1986, Nelson and Hutchings 1987, Colin and Clavijo 1988, Nakata and Hirano 1988, Shanks 1988, Sinclair 1988, Campana et al. 1989, Watson and Davis 1989, Gaughan et al. 1990, Laprise and Dodson 1990, Clarke 1991, Moser and Boehlert 1991), and Leis (1991) who reviewed the larval biology of coral reef fish. However, to the authors' knowledge, there is no published material dealing specifically with the issue of larval export from marine reserves.

There has been considerable debate as to the dispersal function of the pelagic larval phases of fish (e.g. Johannes 1978, Barlow 1981), and two opposing ideas have emerged: the larval drift (Cushing 1986) and the retention (Sinclair 1988) hypotheses, although Sinclair (1988, p. 41) states that "drift itself... is not inconsistent with the concept of larval retention". Campana et al. (1989) documented a case where both mechanisms operated simultaneously and independently for larval haddock on Browns Bank, Nova Scotia.

Distribution and dispersal of larval fish are controlled by both passive transport mechanisms and active behaviour (Norcross and Shaw 1984), and larval dispersal is therefore essentially a process of modulated drift (Power 1984), where final destination is determined by the interactions between the advective (velocity) and diffusive (turbulence) components of the water body and the biological components (buoyancy, active swimming) of the larvae. Available data for coral reef fish suggest that their larvae are active, behaviourally sophisticated animals which may have a considerable degree of control over their dispersal and distribution (Leis 1991). Larvae of perciform fish as small as 4–7 mm in length (SL) are thought to be capable of precise water-column manoeuvring by active swimming, orientation towards physical cues and buoyancy modulation (Richards and Lindeman 1987). However, currents remain a major determinant of larval distribution (Leis and Goldman 1983), and a knowledge of circulation patterns may reveal much about probable dispersal routes and extents of closure systems utilized. While quantitative demonstration of egg and larva dispersal distances is not easily achieved, an idea of their potential for dispersal, or retention, can be inferred from their localized distributional patterns (behaviour) in association with local current regimes.
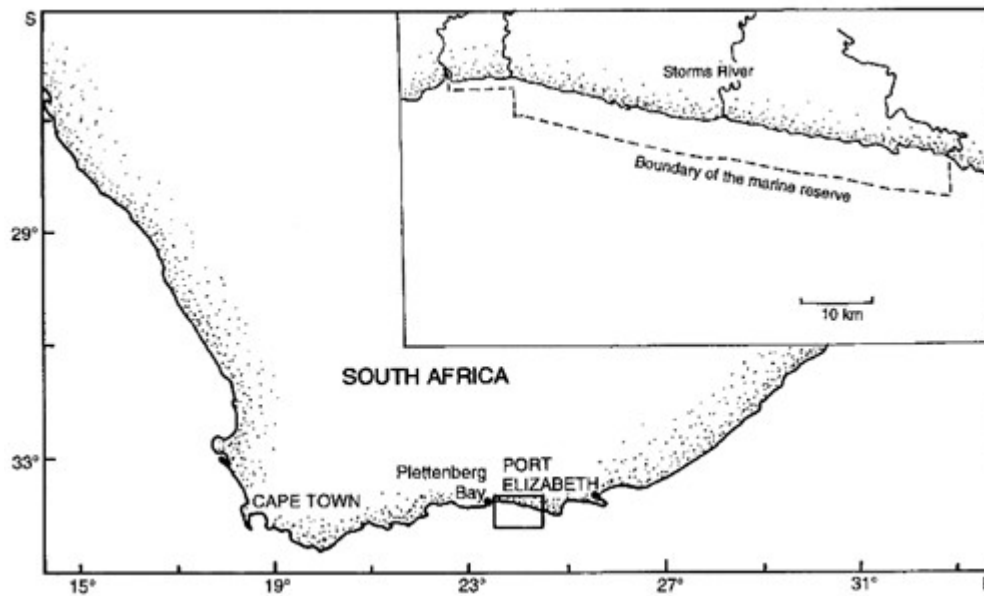
The Tsitsikamma National Park (TNP) is situated along a steeply shelving, exposed part of the South African south coast. It extends 72 km alongshore, with a narrow (c. 0,5 km) terrestrial component incorporating little more than the shoreline, cliffs and cliff-tops, and up to 5 km offshore (c. 100 m depth). The total area of the TNP is approximately 360 km2. The TNP was established in 1964, the first marine reserve to be proclaimed on the African continent. All offshore fishing activity is prohibited in the reserve, but shore-angling is permitted along a short (2,8 km) stretch of coastline adjacent to the rest camp.

Of particular interest to the present study are the larvae of the family Sparidae, of which over 40 species are both recreationally and commercially important in linefisheries along the Cape south coast. At present, several key endemic sparids, including red stumpnose Chrysoblephus gibbiceps, red steenbras Petrus rupestris and white musselcracker Sparodon durbanensis, are considered to be overexploited and highly vulnerable in the Southern Cape linefishery (Van der Elst and Adkin 1991). Most sparids along the Cape south coast occur over areas of high-profile reef between depths of approximately 10 and 100 m. Juvenile habitats are inter- and subtidal, in rock pools, over sandy substrata and abutting reefs, and over reef-fringes, generally in water depth <10 m (van der elst 1981, buxton and smale 1984, van der elst and adkin 1991). potential nursery areas are therefore patchily available within the tnp and throughout the adult distributional ranges along the greater South African coastline.

In this study, densities of larvae over reef and sand patches in the TNP were compared statistically to test for the presence of non-random distribution patterns. Of special interest was whether there was evidence of active retention by reef-associated larvae over areas of reef. These behavioural data, together with inshore ocean circulation information, were used to evaluate the potential of the reserve to seed adjacent areas with larvae.

Methods

Paired 57-cm mouth diameter Bongo nets with 500-mm mesh were used throughout the study. Details of the sampling procedure are presented elsewhere (Tilney and Buxton 1994). The study area was a 15 km stretch of coastline east of Storms River mouth. Four sampling sites were chosen according to substratum type: the Knoll and Rheeders, high-profile reef areas with reef relief generally >5 m;

Sanddrif, a predominantly sandy region with some scattered, low-profile reef; and Elands, a primarily sandy region. Three stations, determined by water depth (20, 40 and 80 m), and running perpendicular to the shore were sampled at each site.
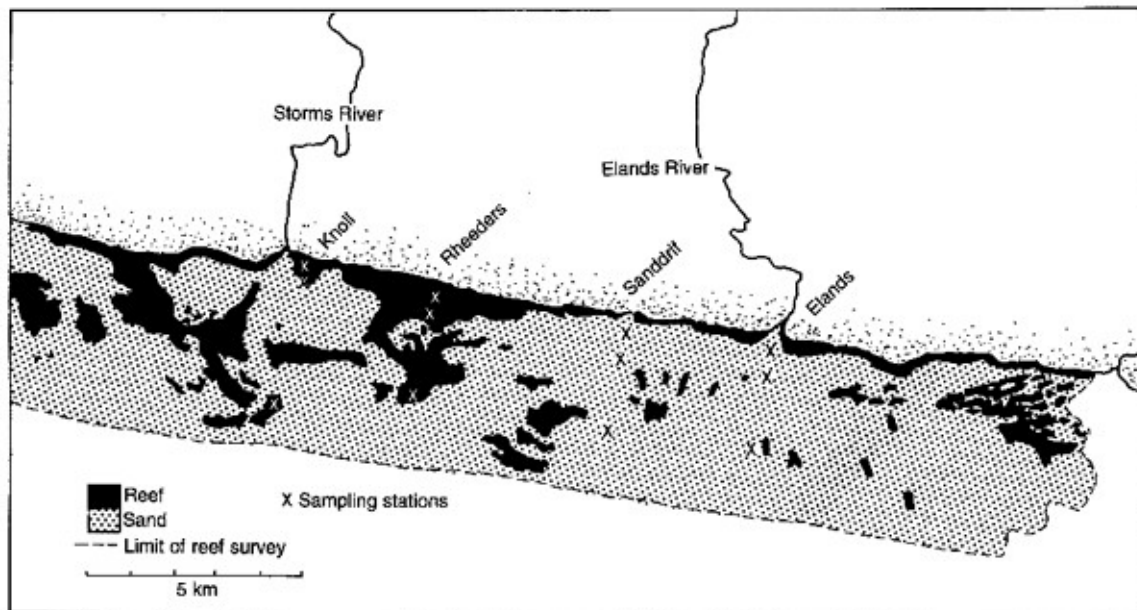
These stations were approximately 0,35, 1,26 and 3,83 km offshore respectively. Horizontal tows were taken 3 m from the surface at each station. At the inshore (0,35 km) stations, a series of deeper (15 m from the surface) horizontal tows was also taken. Sampling took place monthly, weather permitting, and the study comprised 13 trips over an 18-month period between February 1991 and July 1992. However, the sampling area was prone to cold, upwelling events during spring and summer, when larvae were almost entirely absent in the samples. Data from three upwelling-affected sampling months (February, March and April 1992) were excluded from the analysis.

Data analysis

While analysis of larval distribution at species level would have been appropriate for this study, this was not possible because of the relatively small numbers of larvae in the samples. Larval density data from the four most abundant families in the collections were used in the analysis. These were the Gobiesocidae (2 species, n = 374), Blenniidae (3 species, n = 469), Engraulidae (2 species, n = 1 633) and Sparidae (6 species, n = 515). Although 17 sparid species were identified in the samples, only the six most abundant species were chosen for analysis in order to minimize the extent to which species-specific larval behaviour patterns would influence the analysis. For example, larvae from one of the more abundant sparids, Spondyliosoma emarginatum, were excluded on the basis that they produce benthic eggs, a phenomenon atypical of the rest of the sparids in the Tsitsikamma region. Three distinct spawning modes were represented among the four families. Gobiesocids and blenniids are inshore, reef-dwellers with benthic eggs and pelagic larvae, sparids are predominantly inshore, reef-dwellers with pelagic eggs and larvae, and engraulids are offshore, pelagic fish with pelagic eggs and larvae.

Catches of larvae were erratic throughout the year, probably owing to their distributional patchiness, and no marked seasonality of abundance was detected (Tilney and Buxton 1994). Data for all months were therefore pooled. Data for the number of larvae per 100 m3 of water were transformed using x+1 to stabilize the variances and then subjected to analysis of variance (ANOVA). Tests of homogeneity of

the variances were carried out using Levene's test. Differences in the abundance of larvae were tested using Scheffé's multiple range procedures.

The null hypothesis for the study was that there were no significant differences in larval densities between areas of reef and those of sand, between inshore and offshore stations or between sampling depth in the water column.

Sea currents and wind measurement
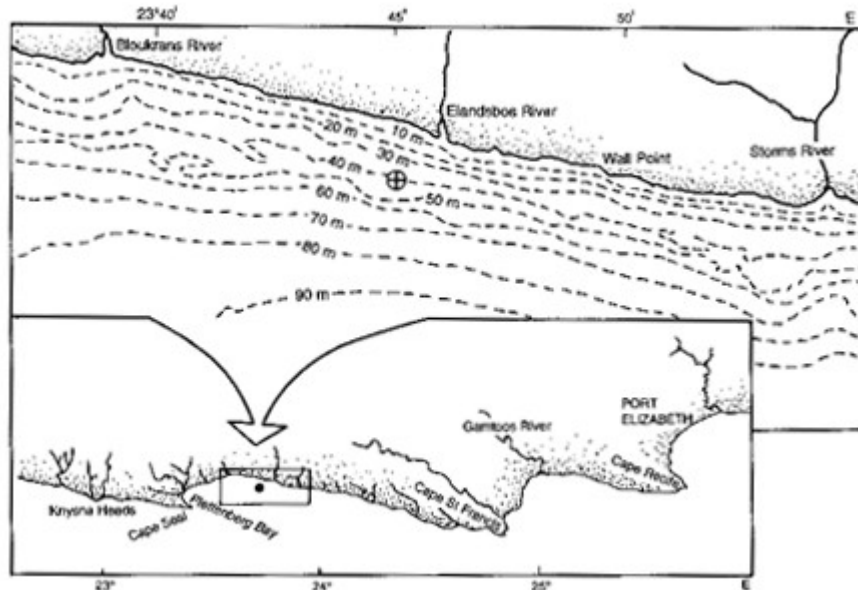
A "Neil Brown" ACM2 acoustic phase-shift current meter was moored at 48 m in 51 m of water at 34° 01,35'S , 23° 43,80'E. This position was chosen because of the near-uniform gradient in bathymetry and the hard base, which ensured that the instrument was not in a sediment passage. The requirements of this work were an identification of periodic motion at subtidal frequencies, having time and distance scales of 2 – 10 days and 10 km respectively, together with drift patterns in different seasons. It was therefore important to eliminate as much current noise as possible.

The instrument was in place from 4 July 1991 to 17 January 1992, yielding 4 767 post-deployment vector-averaged, hourly records. The recording interval was set at 6 minutes. During this period, current was sampled at 25 Hz and vector-averaged internally.

In any shallow-water application, a number of factors can influence the measurement of current. The first is the rectifying characteristic of the sensors in the presence of a swell, normally having a frequency above the Nyquist frequency of sampling. Mooring motion is related to the swell, which can be near resonance on a short array. The second is the cosine response of the device in the presence of a swell. A moderate swell of 1 – 2 m can introduce distortions into mean flow, even at 50 m. The model of current meter used for the experiment is not rectifying because its Nyquist frequency is a few milliseconds and it has a good cosine response. Third, it was anticipated that, at this shallow depth, considerable biological fouling would occur, which indeed was the case. Nevertheless, the meter worked well throughout the period, with sporadic malfunctioning first appearing on 31 December 1991. This could have resulted from biological material settling on the acoustic mirror or transducer heads. However, whereas a rotor device may fail completely because of biological fouling, or show an obvious secular deterioration, an acoustic instrument may continue to function in an apparently perfect way, while introducing a bias in mean flow through differential fouling of the x and y sensor pairs. In

particular, the formation of bubbles on the transducer heads poses a problem. Inspection of the device on recovery and post-deployment calibration indicated that no change had occurred. Consequently, the sudden changes in flow pattern observed in the data were ascribed to real seasonal effects.

Wind records were obtained from a Weather Bureau anemometer at Plettenberg Bay airport, situated approximately 1 km inland and 137 m above sea level. The period covered was from 21 June 1991 to 23 January 1992, bracketing the current-meter deployment. Daily average values of speed and direction were converted to East-West and North-South components, the former making an angle of some 20° with the Tsitsikamma coast and being the component which induces upwelling. A few doubtful hourly records resulted in small uncertainties in the daily averages. These are of little consequence to the low-frequency variation in upwelling wind, typically of 3 – 4 days duration, or to the generation of shelf waves.

Results

Table I: Size ranges (standard length) and approximate flexion lengths (given in parenthesis) of larvae from four families collected in the Tsitsikamma National Park marine reserve. Data are pooled from all four sampling sites (Knoll, Rheeders, Sanddrif and Elands) and given per station (distance offshore) and sampling depth (surface or deep)

Station	Size range (mm) per family			
	Engraulidae (7,3 mm)	Gobiesocidae (4,7 mm)	Sparidae (5,5 mm)	Blenniidae (7,0 mm)
0,35 km, deep	3,2 – 10,5	2,2 – 8,2	2,0 – 8,0	2,8 – 7,6
0,35 km, surface	2,5 – 13,8	2,8 – 9,2	2,1 – 12,8	2,6 – 13,7
1,26 km, surface	2,5 – 7,5	3,3 – 6,2	2,1 – 10,3	2,3 – 19,0
3,83 km, surface	2,0 – 10,4	2,5 – 5,3	1,8 – 13,0	2,4 – 7,6

Most larvae were in the post-yolksac, pre-flexion stage of development, although post-flexion larvae belonging to all four families were present at all sampling localities. Details of the total larval complement captured during the study are presented elsewhere (Tilney and Buxton 1994).

Table II: Total numbers of larvae sampled (N), mean monthly ($\bar{x}$) larval concentrations (numbers·100 m^{-3}) and standard deviation (SD) of engraulids, gobiesocids, sparids and blenniids at four sampling stations at each of the four sample sites in the Tsitsikamma National Park. Data are combined for all months

Station	Family	Number of larvae·100 m^{-3} per sampling site											
		Knoll			Rheeders			Sanddrif			Elands		
		N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD
0,35 km, deep	Engraulidae	46,68	2,33	3,46	34,43	1,72	2,28	18,33	0,92	1,78	35,91	1,80	3,85
	Gobiesocidae	89,26	4,46	4,54	157,26	7,86	14,85	9,49	0,47	0,85	16,89	0,84	1,71
	Sparidae	36,70	1,80	2,70	24,40	1,20	2,00	17,50	0,90	1,05	17,00	0,80	0,80
	Blenniidae	21,27	1,06	1,31	38,85	1,94	3,94	15,60	0,78	1,03	28,07	1,40	2,13
0,35 km, surface	Engraulidae	39,53	1,98	3,06	23,37	1,17	2,31	35,14	1,76	2,22	82,07	4,10	8,89
	Gobiesocidae	11,25	0,56	1,03	24,57	1,23	2,63	17,17	0,86	1,42	26,73	1,34	3,38
	Sparidae	20,40	1,00	2,50	27,90	1,40	1,90	81,30	4,10	9,70	12,90	0,60	0,70
	Blenniidae	18,06	0,90	1,55	58,02	2,90	4,53	58,90	2,95	3,93	70,54	3,53	7,20
1,26 km, deep	Engraulidae	101,55	5,08	8,09	56,13	2,81	4,45	136,35	6,82	9,37	221,39	11,17	23,27
	Gobiesocidae	0	0	0	3,23	0,16	0,32	2,45	0,12	0,37	10,63	0,53	1,60
	Sparidae	18,70	0,90	1,60	26,10	1,30	2,20	37,00	1,90	3,00	43,60	2,20	3,30
	Blenniidae	12,72	0,64	1,22	53,28	2,66	3,80	12,15	0,61	1,03	18,64	0,93	1,14
3,83 km, surface	Engraulidae	175,36	8,77	18,99	73,21	3,66	5,30	317,01	15,85	29,94	237,00	11,94	24,31
	Gobiesocidae	2,89	0,14	0,44	1,68	0,08	0,37	0	0	0	0,81	0,04	0,18
	Sparidae	17,40	0,90	1,50	40,30	2,00	3,80	28,20	1,40	1,60	65,90	3,30	5,50
	Blenniidae	9,81	0,49	0,98	10,30	0,52	1,02	30,65	1,53	4,06	11,93	0,60	0,73

The total and mean monthly larval concentrations taken at the four stations at each of the four sample sites, representing a total of 2 991 larvae from 160 samples, are presented in Table II. No significant differences in larval abundance were found over the four sample sites for all four families (p > 0,9448 in each case, Levene's test p > 0,8732). Therefore, when testing for sand v. reef distributions, larval abundances from the two reef sites (Knoll and Rheeders) were combined. Similarly, the data for the two sand sites (Sanddrif and Elands) were combined. The probabilities of Type-II error for each family were less than 0,17 for differences in the means exceeding 0,5.

The ANOVA revealed several trends.

Table III: Comparison of larval abundance (number·100 m^{-3}) between surface and deep samples taken over reef and sand at the 0,35 km station in the Tsitsikamma National Park. The sample size was 40 in each case

Family	Reef		Sand	
	Deep	Surface	Deep	Surface
Gobiesocidae	246,52**	35,82	26,38	43,90
Blenniidae	60,12	76,08	43,67	129,44*
Sparidae	61,10	48,30	34,50	94,20
Engraulidae	81,11	62,90	54,24	117,21

* = $p < 0,05$
** = $p < 0,01$

(i) Gobiesocids were more abundant at depth than near the surface over reef (F = 15,44, df = 1,78, p = 0,0002); blenniids were more abundant near the surface than at depth over sand (F = 5,80, df = 1,78, p = 0,0184); engraulids and sparids were homogeneously distributed in the water column. These results were confirmed using a non-parametric Kruskal-Wallis test, which suggest that active vertical positional preferences were displayed in the water column by gobiesocids and blennies, but not by sparids or engraulids (See Table III).

Table IV: Comparison of larval abundance (number·100 m^{-3}) with respect to distance offshore in the Tsitsikamma National Park. Sample size in parenthesis

Family	Distance offshore		
	0,35 km (80)	1,26 km (40)	3,83 km (40)
Gobiesocidae	79,22**	16,31	5,38
Blenniidae	205,52**	96,79	62,69
Sparidae	142,50	125,40	151,54
Engraulidae	180,11	515,42	802,58**

** = $p < 0,01$

(ii) Gobiesocids and blenniids were significantly more abundant inshore (F = 12,32, df = 2,237, p < 0,001 and F = 7,65, df = 2,237, p = 0,0006 respectively). Scheffé's multiple range tests revealed significant differences (p < 0,01) between 0,35 km and 1,26 km and between 0,35 km and 3,83 km distances for both Gobiesocidae and Blenniidae. Engraulids were more abundant offshore, with a significant difference between the 0,35 km and 3,83 km distances offshore (F = 5,72, df = 2,237, p = 0,0037). The results were confirmed using the Kruskal-Wallis test. Sparids were homogeneously distributed with respect to distance offshore (See Table IV).

Table V: Comparison of larval abundance (number·100 m^{-3}) between reef and sand stations in the Tsitsikamma National Park. Both sample sizes were 120

Family	Reef	Sand
Gobiesocidae	285,57**	83,36
Blenniidae	202,20	203,90
Sparidae	154,20	209,30
Engraulidae	301,69	529,19

** = $p < 0,01$

(iii) In this analysis the 3,83 km stations were excluded because of uncertainty of substratum type. Gobiesocids were significantly more abundant over reef than over sand (F = 8,56, df = 1,238, p = 0,0038). Engraulids appeared to be more abundant over sand than over reef, but the difference was not significant (p = 0,0937). Blenniids and sparids were homogeneously distributed with respect to substratum type. The results were confirmed using the Kruskal-Wallis test (See Table V).

Currents and winds

Factors which influence currents in the reserve area are wind, tides and the density stratification. Wind operates in a dual role to produce upwelling when the orientation is suitable, so altering the baroclinic component of current, and to produce coastal-trapped waves (CTWs). The latter are not critically dependent on the orientation of the wind and are present throughout the year. They are induced by east-moving weather systems (Schumann and Brink 1990). The period of a first mode wave is typically four days in the study area.

A general discussion of tides and inertial currents around South Africa has been presented by Schumann and Perrins (1983). On the small scale discussed herein, spectral analysis of the current-meter record shows that most of the energy is in the form of CTWs generated by synoptic weather patterns. Rotary analyses of the original hourly records and the filtered series with tides removed shows that there is a small tidal contribution in the cross-shelf direction, with average onshore and offshore speeds of 0,2 and 0,1 cm.s–1 respectively. By contrast, the longshore CTW component is an order of magnitude larger.

The larger features of the thermohaline structure on the Agulhas Bank have been discussed by Swart and Largier (1987), Schumann and Beekman (1984), Schumann et al. (1982) and Boyd and Shillington (1994). In the Tsitsikamma reserve area, the most important thermohaline process is coastal upwelling, although Swart and Largier (1987) suggest that Agulhas Current tongues may impinge on the coastal region. Isotherms, and hence isopycnals, tilt upwards towards the coast in winter (see Fig. 1 of Swart and Largier 1987). This would induce a westward baroclinic component of flow over some 20 km in midwater, which would be enhanced closer to the coast in the summer when almost contiguous upwelling events occur.

By far the dominant physical process in the TNP marine reserve area is CTW events. These are apparent in the filtered time-series and their spectra, which show peaks near 2,5 and 5 days, the latter being the more energetic, with peak amplitudes of 17 cm.s–1 traceable to the longshelf time-series and 6 cm.s–1 to the cross-shelf time-series. Currents recorded 25 m deep in this area during March and

April 1991 were primarily longshore with a maximum speed of 19 cm.s–1, averaging 6 cm.s–1 (E. H. Schumann, University of Port Elizabeth, pers. comm.).
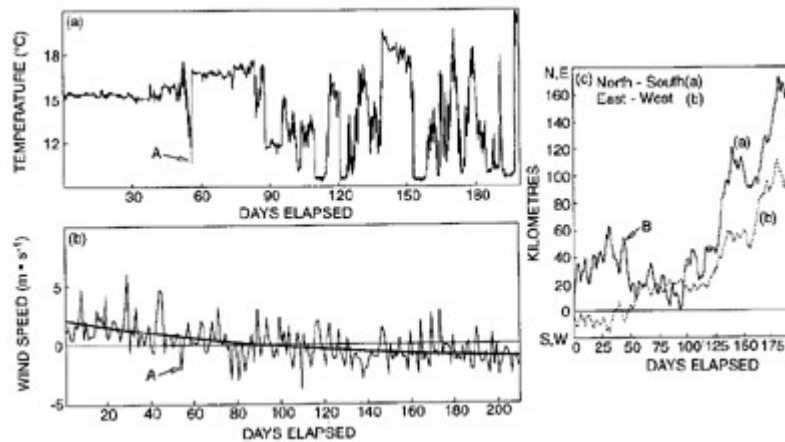

Time-series of temperature, wind and currents at the current-meter site are shown in Figure 4. The series start on 4 July 1991 and are 198 days long. Their most striking feature is the secular change in the eastward component of wind as the belt of westerlies moves south as winter progresses to summer. A quadratic trend line fitted to the series crosses the zero line on Day 97 (9 October). Thereafter, the wind was on average westwards and more favourable to upwelling. This is apparent in the temperature time-series (See Fig. 4a). After Day 85 (27 September) upwelling events became almost contiguous, with 6°C depressions from the winter constant value of 15°C. A temperature time-series from a recorder in 12 m of water at Storms River mouth shows corresponding sharp, but short-lived, depressions (M. J. Roberts, Sea Fisheries Research Institute, pers. comm.), indicating that the temperature effects of upwelling are more sustained at 48 m.

The effect labelled "A" in Figure 4a has its corresponding cause at "A" in Figure 4b. Further along the time-series, such pulses of eastward wind are less coherent with cooling because the ocean has its own free modes of motion which are not necessarily in phase with atmospheric forcing.

Figure 4c shows the component displacements, giving the total displacement of a particle under spatially homogeneous current conditions. Over the 198 days, these displacements were 157 and 87 km in the North-South and East-West directions respectively, with speeds of 0,793 and 0,439 km.day–1 respectively. This corresponds to a vector drift velocity of 1 km.day–1 at 60° east of north, a direction from the current-meter site across the bathymetry towards the mouth of the Elandsbos River (see Fig. 3).
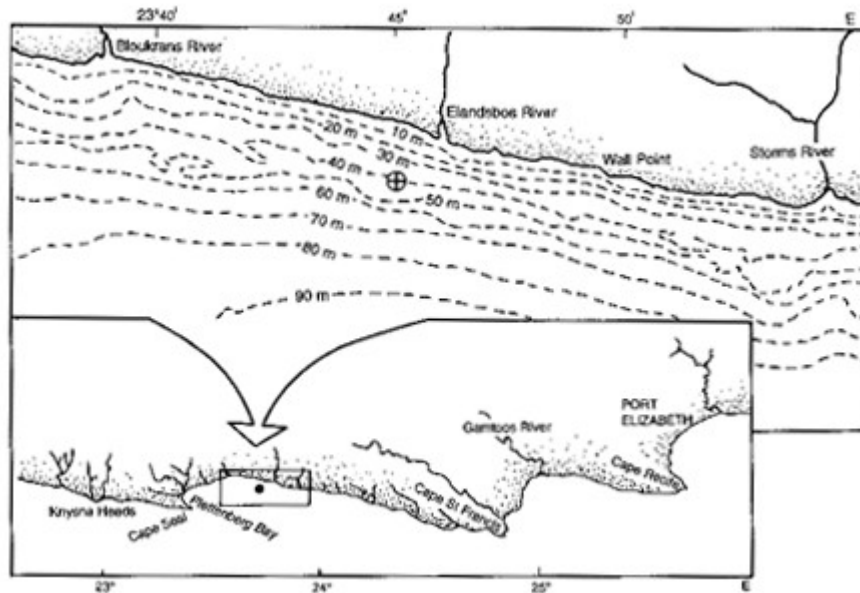
Prior to Day 85, the current was oriented more to the east and was weaker. Thereafter, when upwelling started, the current was oriented more towards the coast, and therefore in compensation for upwelling. The latter part of the time-series yielded a value of around 2 cm.s–1 for the upwelling compensation. Whether this comparatively strong current is characteristic of the whole reserve area or is a feeder current at a preferential site, is a question which is unanswerable with the available data. A case of preferential access on the West Coast near the Olifants River has been documented by Dingle and Nelson (1993).

The peaks in the displacement graphs represent the CTW events. These are integrated into the ambient flow. Strong events such as that labelled "B" in Figure 4c would result in a to-and-fro motion of passive material, spanning 60 km within 8 days.

Discussion

Non-random distributional patterns were found for three of the four families of larvae under investigation in the TNP, those of gobiesocids and blenniids being particularly well defined. Representatives of those two families are characteristically small, cryptic, benthic animals which seldom venture above, or away from, the protective reef habitats with which they are intimately associated. Gobiesocid larvae were more abundant at depth than near the surface, whereas blenniid larvae were more abundant near the surface than at depth, suggesting that they exhibited active vertical positioning in the water column. The greater abundance of gobiesocid larvae over reef than over sand, and at the most nearshore sites, indicated that they were able to overcome the dispersive forces associated with their pelagic environment and maintain a close association with areas of reef throughout their larval phase. That both young and old larvae were present in the collections (see Table I) supports this belief. Blenniid larvae exhibited a strong inshore distribution pattern, and their preference for a near-surface habitat probably accounted for their lack of affinity for either rocky or sandy substrata. Leis (1994) found that the production of non-pelagic eggs was the single most important factor in determining larval retention in atoll lagoons, and both gobiesocids and blenniids produce adhesive, benthic eggs which are laid directly onto rock or shell surfaces, where they remain until hatching (Thresher 1984). Dispersal during this developmental phase is therefore effectively countered. In addition, larvae hatching from non-pelagic eggs are generally larger and have better developed sensory and swimming abilities than larvae from pelagic eggs (Leis 1994).

Sparids are robust, supra-benthic animals that occupy substantially larger home-ranges than the smaller gobiesocid and blenniid species. Post-settlement juveniles of several sparids occupy intertidal rock pools (Beckley 1985a, b), whereas others occur subtidally over sandy substrata in close association with reef (Buxton and Smale 1984, Van der Elst and Adkin 1991). The distribution of sparid larvae in this study was entirely homogeneous, suggesting that they did not exercise preferred position retention in the water and, by implication, that they were more prone to the dispersive properties of the water body surrounding them. Therefore, it may be valid to project probable dispersal distances for sparid larvae in the Tsitsikamma region on the basis of local current-circulation patterns. The absence of active position retention during the sparid larval phase would imply that either the nature of local circulation is such that settlement-stage larvae occur close enough inshore to allow settlement directly on to their sandy, reef-fringe nursery areas, or that they are able to migrate actively inshore to the nursery areas during the late larval or early juvenile phases.

Engraulids are small, schooling species which are pelagic throughout their life cycle and their distribution is not expected to be influenced by substratum type. Their distribution is likely to become progressively more patchy at the onset of fin differentiation when mobility improves and they begin aggregating into schools (Armstrong and Thomas 1989). On the west coast of South Africa, the nursery areas for clupeid and engraulid larvae and juveniles are distant from the spawning grounds (Armstrong and Thomas 1989). The dispersal of these larvae, which have estimated swimming speeds of approximately 1–3 cm.s–1, is believed to be largely passive in the Benguela system where northward-bound surface current speeds average 39 cm.s–1. However, using models of flow for the St Helena Bay area, Nelson and Hutchings (1987) were able to demonstrate that, even at such slow swimming speeds, onshore swimming activity could significantly enhance recruitment of larvae 1–2 weeks old (c. 6–10 mm) to the St Helena Bay current-closure system, a major juvenile nursery area for these species. Engraulid spawning on the shelf-break of the eastern Agulhas Bank, approximately 90 km offshore, has been well documented (Hampton 1992, Roel et al. 1994), and although little is known about the distribution or movement of pre-recruits in this region, local recruitment is thought likely there (Roel et al. 1994). The engraulid larvae encountered in the present study may therefore complete their entire life-cycle on the continental shelf along the South-East Coast, possibly sharing a current-closure system with inshore pelagic spawners such as sparids. Although it has been speculated that engraulids may spawn close inshore in Algoa Bay (Beckley 1986), not a single engraulid egg was found in the Tsitsikamma region during the present study, suggesting that inshore spawning does not occur there.
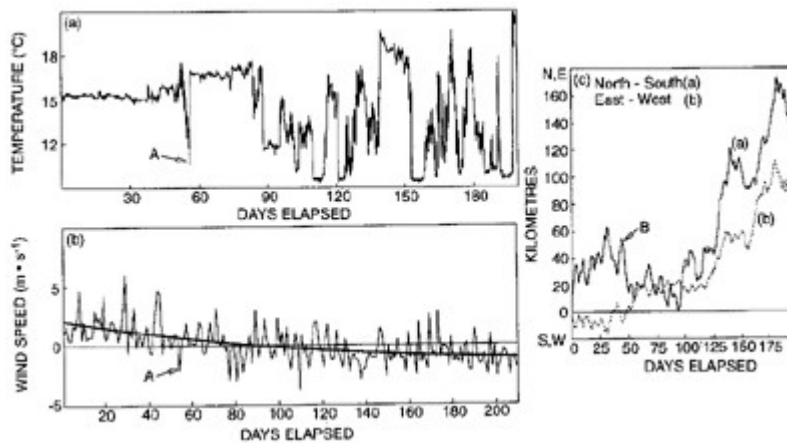
The current-meter data indicated that there were two distinct current patterns in the Tsitsikamma area, one during winter and another during spring and summer. The winter data revealed a fairly regular

longshore current oscillation, brought about by a band of east- moving cyclones that occur over southern South Africa at that time of year. Such weather systems propagating eastwards alter sea level and generate barotropic waves with periods of 2–4 days. The process is strong in winter; it also occurs in summer, but less frequently. These barotropic current reversals are strongest inshore, and decrease in frequency and intensity with distance offshore (Schumann 1987). The current-meter data revealed maximum current speeds of 17 cm.s–1 at a depth of 48 m, translating to a rate of travel of 14,7 km.day–1. The amplitude of oscillatory displacement for drifting biotic material caught up in the currents at this depth would therefore be of the order of 30–60 km in a longshore direction. As the TNP has a longshore dimension of approximately 70 km, larvae drifting passively would therefore be dispersed beyond its borders. However, the distributions in this study revealed that larvae were not passive drifters (except, perhaps, for sparids) and their dispersal in these nearshore waters during winter would be slight.

Wind effects may play a more important and direct role in larval transport in the surface layer where current velocities may be substantially greater than at depth. Only the stronger winds are capable of changing current direction and there is a time-lag of about one day before current reversal. As wind stress is generally taken as being proportional to the square of wind speed, small increases in wind speed result in significant increases in stress (Schumann 1987). When strong wind conditions occur in sympathy with the barotropic currents, dispersal distances for larvae in the surface layer above the thermocline may be substantially enhanced. Drift-card studies have demonstrated a maximum rate of travel of 26 km.day–1 in summer and 18 km.day–1 in winter inshore off the south and south-west coasts of South Africa (Duncan and Nell 1969, Shelton and Kriel 1980).
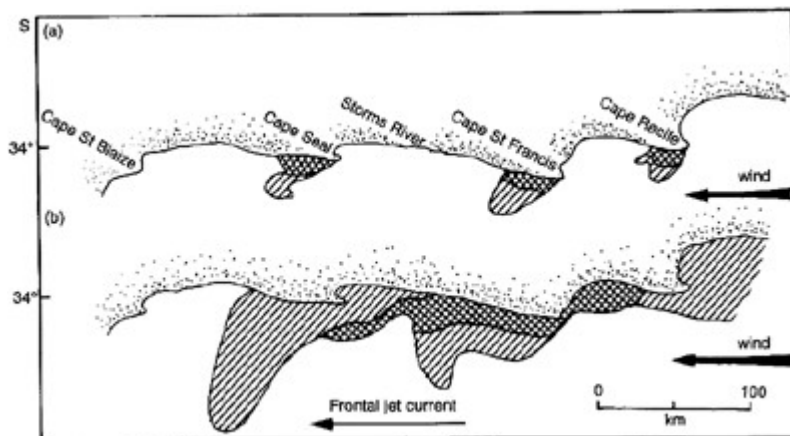

The massive surface water displacement along the Tsitsikamma coast during upwelling events in spring and summer is likely to impact considerably on plankton dispersal. Satellite images reveal tongues of cold, upwelled water extending offshore in the lee of the capes along the Southern Cape coast (See Fig. 5) during these events. As warm surface water is forced offshore ahead of the cold upwelled water, the plankton within it may be displaced considerable distances away from the coast. Pelagic elements within the upwelled water would be similarly displaced offshore. The decline in larval numbers sampled during, and shortly after, upwelling events in the TNP (Tilney and Buxton 1994) supports that hypothesis. All larval families were affected, indicating that the upwelling-associated currents were strong enough to displace those that displayed strong retentive abilities, such as the gobiesocids.

At the interface between cold upwelled water and warmer surface water a longshore jet-current becomes established in sympathy with the wind (Schumann et al. 1982), which would tend to displace pelagic biota in a south-westerly direction. If the upwelling is of short duration (3–4 days), the cold

water may extend only 30–40 km offshore and a few tens of kilometres longshore, but if it persists for a longer period (10–12 days), upwelled water may be transported up to 75 km offshore and as much as 200–250 km south-westwards. When the easterly winds subside, there is generally a swing back to a westerly wind condition, resulting in the dissipation of the upwelling process. Downwelling occurs and the warm, surface waters move back inshore. Eggs and larvae originating in the TNP are therefore likely to be transported considerable distances both offshore and longshore during upwelling events. When the upwelling process dissipates, there is onshore water movement and eggs and larvae may be transported back inshore, to a position considerably west of their origin. While there is some evidence that inshore and shelf-edge currents counter to the Agulhas Current operate along the eastern Agulhas Bank (Baird 1970, in Schumann 1987, Shannon 1970, Boyd et al. 1992, Hutchings 1994), there is also evidence that they are not permanent and that both inner- and outer-shelf counter-currents are variable throughout the year (Schumann 1987, Boyd and Shillington 1994).

The continental shelf-break along the Tsitsikamma coast is approximately 90 km offshore, and it is possible that some of the eggs and larvae carried offshore during upwelling events may become entrapped by the Agulhas Current. If they are, they may either be returned to the continental shelf in the vicinity of the Agulhas Bight, south of Mossel Bay, where Agulhas Current water frequently intrudes onto the shelf (Boyd and Shillington 1994), or they may remain in the current and be permanently lost to the system (sensu Sinclair 1988). In an ichthyoplankton survey between Algoa Bay and the Tugela River, Beckley (1993) revealed that although sparid larvae occurred all the way out to the shelf-break, they were not found in the Agulhas Current itself. Boyd and Shillington (1994) demonstrated a link between the inshore, summer upwelling events along the Cape south coast and the establishment of a near-surface, cool-water ridge on the central Agulhas Bank, south of Mossel Bay. A cyclonic circulation pattern is prevalent around this cool-water ridge, with a dominant inshore eastward component and an offshore, south-westward flow along its margin (Hutchings 1994, Probyn et al. 1994). The extent of that ridge may well define the westward limit of the upwelling-associated dispersal for sparid larvae and other planktonic biota of inshore origin along the Cape south coast.
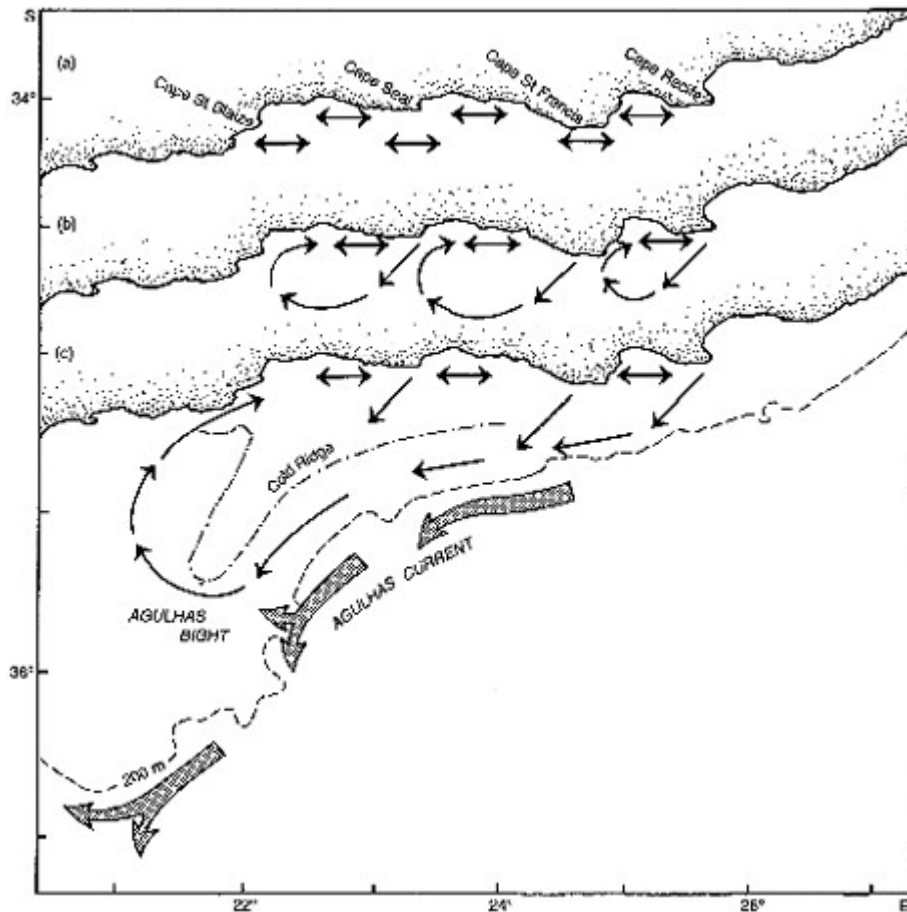
A summary of three theoretical current-closure systems for eggs and larvae originating in the TNP is presented in Figure 6. The first of these is a longshore, barotropic oscillation, generated by coastal trapped waves and typical of winter. Based on current- meter data, larval transport distances of between 30 and 60 km would be expected (See Fig. 6a). The second and third scenarios are typical of spring and summer, when upwelling events disrupt the longshore current oscillation pattern. Based on satellite imagery, baroclinic, surface-layer transport of larvae over distances of approximately 30–40 km offshore and longshore would be probable during short-lived upwelling events. Downwelling and the return of warm, surface water inshore would complete the current closure. During prolonged upwelling events the same scenario is envisaged, but on a larger scale. Dispersal distances of 70–90 km offshore and 200–250 km longshore, and bounded in the west by the cool-water ridge off Mossel Bay, may be realized. This theory remains untested, however, and its elucidation would require extensive drogue studies in the region.

In conclusion, the present results demonstrate that blenniid and gobiesocid larvae adopt a strategy of active, inshore position retention within the TNP marine reserve. On the other hand, the distribution of sparid larvae was diffuse, suggesting that theirs was a strategy more aligned with passive dispersal. Such information, together with that of the current patterns of the region, suggested that, although export of sparid larvae from the TNP marine reserve was a probability, such export would take place over only fairly short distances. The current- meter data did not reveal information about the near-surface water movement, where substantially greater dispersal potential may reside. The extent of the current-closure system for larvae of inshore origin, e.g. sparids, would therefore appear to be controlled by oscillating longshore barotropic currents in winter, and by baroclinic cross- and longshore surface currents, associated with upwelling events, during spring and summer.

Although the magnitude of export of pelagic biota from the TNP to adjacent, exploited areas could not be quantified, it is likely to be substantial. This is because the peak spring spawning season for many important commercial and recreational linefish species along the Cape south coast (Buxton and Clarke 1989, 1991, Buxton 1990, Mann 1992) coincides with the commencement of the upwelling season in September/ October, the period when the potential for dispersal of eggs and larvae is greatest. Also, larval survival is likely to be substantially enhanced by the high primary productivity (Probyn et al. 1994) associated with post-upwelling periods in the area. The TNP marine reserve harbours large populations of reproductively active linefish (Buxton and Smale 1989) and, from a fishery recruitment point of view, it may indeed have been serendipitous that this reserve was established within a major upwelling cell.

Acknowledgements

Literature Cited

ANON. 1990 — The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. NOAA Tech. Memo. NMFS-SEFC 261: 40 pp.

ARMSTRONG, M. J. and R. M. THOMAS 1989 — Clupeoids.
In Oceans of Life off Southern Africa. Payne, A. I. L. and R. J. M. Crawford (Eds).
Cape Town; Vlaeberg: 105–121.

BARLOW, G. W. 1981 — Patterns of parental investment, dispersal and size among coral-reef fishes.
Environ. Biol. Fishes 6(1): 65–85.

BECKLEY, L. E. 1985 — The fish community of East Cape tidal pools and an assessment of the nursery function of this habitat.
S. Afr. J. Zool. 20(1): 21-27.

BECKLEY, L. E. 1985 — Tide-pool fishes: recolonization after experimental elimination.
J. expl mar. Biol. Ecol. 85(3): 287–295.

BECKLEY, L. E. 1986 — The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish.
S. Afr. J. Zool. 21(3): 244–252.

BECKLEY, L. E. 1993 — Linefish larvae and the Agulhas Current.
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: 57–63.

BENNETT, B. A. and C. G. ATTWOOD 1991 — Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa.
Mar. Ecol. Prog. Ser. 75(2&3): 173–181.

BENNETT, B. A., ATTWOOD, C. G. and C. L. GRIFFITHS 1989 — Focus on galjoen. Preliminary tagging results.
Tagging News 5: 8–9.

BOYD, A. J. and F. A. SHILLINGTON 1994 — Physical forcing and circulation patterns on the Agulhas Bank.
S. Afr. J. Sci. 90(3): 114–122.

BOYD, A. J., TAUNTON-CLARK, J. and G. P. J. OBERHOLSTER 1992 — Spatial features of the near-surface and midwater circulation patterns off western and southern South Africa and their role in the life histories of various commercially fished species.
In Benguela Trophic Functioning. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds).
S. Afr. J. mar. Sci. 12: 189–206.

BUXTON, C. D. 1987 — Life history changes of two reef fish species in exploited and unexploited marine environments in South Africa.
Ph.D. thesis, Rhodes University: vii + 215 pp.

BUXTON, C. D. 1990 — The reproductive biologyof Chrysoblephus laticeps and C. cristiceps (Teleostei: Sparidae).
J. Zool., Lond. 220: 497–511.

BUXTON, C. D. and J. C. ALLEN 1989 — Mark and recapture studies of two reef sparids in the Tsitsikamma Coastal National Park.
Koedoe 32(1): 39–45.

BUXTON, C. D. and J. R. CLARKE 1989 — The growth of Cymatoceps nasutus (Teleostei: Sparidae), with comments on diet and reproduction.
S. Afr. J. mar. Sci. 8: 57–65.

BUXTON, C. D. and J. R. CLARKE 1991 — The biology of the white musselcracker Sparodon durbanensis (Pisces: Sparidae) on the Eastern Cape coast, South Africa.
S. Afr. J. mar. Sci. 10: 285–296.

BUXTON, C. D. and M. J. SMALE 1984 — A preliminary investigation of the marine ichthyofauna in the Tsitsikamma Coastal National Park.
Koedoe 27: 13–24.

BUXTON, C. D. and M. J. SMALE 1989 — Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the Southern Cape coast.
J. appl. Ecol. 26: 441–451.

CAMPANA, S. E., SMITH, S. J. and P. C. F. HURLEY 1989 — A drift-retention dichotomy for larval haddock (Melanogrammus aeglefinus) spawned on Browns Bank.

Can. J. Fish. aquat. Sci. 46: 93–102.

CLARKE, T. A. 1991 — Larvae of nearshore fishes in Oceanic Waters near Oahu, Hawaii. Tech. Rep. NOAA NMFS 101: 19 pp.

COLIN, P. L. and I. E. CLAVIJO 1988 — Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, southwestern Puerto Rico.
Bull. mar. Sci. 43(2): 249–279.

CUSHING, D. H. 1986 — The migration of larval and juvenile fish from spawning ground to nursery ground. J. Cons. perm. int.
Explor. Mer 43: 43–49.

DINGLE, R. V. and G. NELSON 1993 — Sea-bottom temperature, salinity and dissolved oxygen on the continental margin off south-western Africa.
S. Afr. J. mar. Sci. 13: 33–49.

DUNCAN, C. P. and J. H. NELL 1969 — Surface currents off the Cape coast.
Investl Rep. Div. Sea Fish. S. Afr. 76: 19 pp.

GARCÍA-RUBIES, A. and M. ZABALA 1990 — Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands marine reserve (NW Mediterranean).
Scientia Mar., Barcelona. 54(4): 317–328.

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.

HAMPTON, I. 1992 — The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf.
In Benguela Trophic Functioning. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds).
S. Afr. J. mar. Sci. 12: 1031–1050.

HUTCHINGS, L. 1994 — The Agulhas Bank: a synthesis of available information and a brief comparison with other east-coast shelf regions.
S. Afr. J. Sci. 90: 179–185.

JOHANNES, R. E. 1978 — Reproductive strategies of coastal marine fishes in the tropics.
Environ. Biol. Fishes 3: 65–84.

LAPRISE, R. and J. J. DODSON 1990 — The mechanism of retention of pelagic tomcod, Microgadus tomcod, larvae and juveniles in the well-mixed part of the St. Lawrence Estuary.
Environ. Biol. Fishes 29: 293–302.

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).
New York; Academic Press: 183–230.

LEIS, J. M. 1994 — Coral sea atoll lagoons: closed nurseries for the larvae of a few coral reef fishes.
Bull. mar. Sci. 54(1): 206–227.

LEIS, J. M. and B. GOLDMAN 1983 — Studies on the biology of larval fishes in the Lizard Island area, Northern Great Barrier Reef.
In Proceedings: Inaugural Great Barrier Reef Conference. Baker, J. T., Carter, R. M., Sammarco, P. W. and K. P. Stark (Eds).
Townsville; James Cooke University Press: 221–225.

MANN, B. Q. 1992 — Aspects of the biology of two inshore sparid fishes (Diplodus sargus capensis and Diplodus cervinus hottentotus) off the south-east coast of South Africa.
M.Sc. thesis, Rhodes University, Grahamstown:125 pp.

MOSER, H. G. and G. W. BOEHLERT 1991 — Ecology of pelagic larvae and juveniles of the genus Sebastes.
Environ. Biol. Fishes 30: 203–224

NAKATA, H. and T. HIRANO 1988 — Wind effects on the transport of red sea bream larvae from a coastal spawning ground adjacent to Shijiki Bay.
Nippon Suisan Gakkaishi 54(9): 1545–1552.

NELSON, G. and L. HUTCHINGS 1987 — Passive transportation of pelagic system components in the southern Benguela area.
In The Benguela and Comparable Ecosystems. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds).
S. Afr. J. mar. Sci. 5: 223–234.

NORCROSS, B. L. and R. F. SHAW 1984 — Oceanic and estuarine transport of fish eggs and larvae: a review.
Trans. Am. Fish. Soc. 113(2): 153–165.

POWER, J. H. 1984 — Advection, diffusion, and drift migrations of larval fish.
In Mechanisms of Migration in Fishes. McCleave, J. D., Arnold, G. P., Dodson, J. J. and W. H. Neill (Eds).
New York; Plenum: 27–38 (NATO Conference Series 4. Marine Science 14).

PROBYN, T. A., MITCHELL-INNES, B. A., BROWN, P. C., HUTCHINGS, L. and R. A. CARTER 1994 — A review of primary production and related processes on the Agulhas Bank.
S. Afr. J. Sci. 90: 166–173.

RICHARDS, W. J. and K. C. LINDEMAN 1987 — Recruitment dynamics of reef fishes: planktonic processes, settlement and demersal ecologies, and fishery analysis.
Bull. mar. ·Sci. 41(2): 392–410.

ROBERTS, C. M. and N. V. C. POLUNIN 1991 — Are marine reserves effective in management of reef fisheries?
Rev. Fish Biol. Fish. 1: 65–91.

ROEL, B. A., HEWITSON, J. [D.], KERSTAN, S. and I. HAMPTON 1994 — The role of the Agulhas Bank in the life cycle of pelagic fish.
S. Afr. J. Sci. 90: 185–196.

SCHUMANN, E. H. 1987 — The coastal ocean off the east coast of South Africa.

Trans. R. Soc. S. Afr. 46(3): 215–228.

SCHUMANN, E. H. and L. J. BEEKMAN 1984 — Ocean temperature structures on the Agulhas Bank.
Trans. R. Soc. S. Afr. 45(2): 191–203.

SCHUMANN, E. H. and K. H. BRINK 1990 — Coastal-trapped waves off the coast of South Africa: generation, propagation and current structures.
J. phys. Oceanogr. 20: 1206–1218.

SCHUMANN, E. H. and L-A. PERRINS 1983 — Tidal and inertial currents around South Africa.
In Proceedings of the Eighteenth International Conference on Coastal Engineering, Cape Town, November 1982.
New York; American Society of Civil Engineers: 2562–2580.

SCHUMANN, E. H., PERRINS, L-A. and I. T. HUNTER 1982 — Upwelling along the south coast of the Cape Province, South Africa.
S. Afr. J. Sci. 78(6): 238–242.

SHANKS, A. L. 1988 — Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish.
Fishery Bull., Wash. 86: 703–714.

SHANNON, L. V. 1970 — Oceanic circulation off South Africa.
Fish. Bull. S. Afr. 6: 27–33.

SHELTON, P. A. and F. KRIEL 1980 — Surface drift and the distribution of pelagic-fish eggs and larvae off the south-east coast of South Africa, November and December 1976.
Fish. Bull. S. Afr. 13: 107–109.

SINCLAIR, M. 1988 — Marine Populations. An Essay on Population Regulation and Speciation.
Washington Sea Grant Program, Seattle; University of Washington Press: 252 pp.

SMITH, W. G. and W. W. MORSE 1985 — Retention of larval haddock Melanogrammus aeglefinus in the Georges Bank region, a gyre-influenced spawning area.
Mar. Ecol. Prog. Ser. 24: 1–13.

SWART, V. P. and J. L. LARGIER 1987 — Thermal structure of Agulhas Bank water.
In The Benguela and Comparable Ecosystems. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds).
S. Afr. J. mar. Sci. 5: 243–253.

THRESHER, R. E. 1984 — Reproduction in Reef Fishes.
Neptune City; T. F. H. Publications: 399 pp.

TILNEY, R. L. and C. D. BUXTON 1994 — A preliminary ichthyoplankton survey of the Tsitsikamma National Park.
S. Afr. J. Zool. 29(3): 204–211.

VAN DER ELST, R. P. 1981 — A Guide to the Common Sea Fishes of Southern Africa.
Cape Town; Struik: 367 pp.

VAN DER ELST, R. P. and F. ADKIN (Eds) 1991 — Marine linefish. Priority species and research objectives in southern Africa.
Spec. Publ. oceanogr. Res. Inst. S. Afr. 1: 132 pp.

WATSON, W. and R. L. DAVIS 1989 — Larval fish diets in shallow coastal waters off San Onofre, California.
Fishery Bull., Wash. 87: 569–591.