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Early developmental stages of the Indian mackerel *Rastrelliger kanagurta* (Cuvier) along the Kerala - Mangalore coast of southeastern Arabian Sea

G. Sree Renjima, V. N. Sanjeevan*, B. R. Smitha, C. B. Lalithambika Devi and M. Sudhakar.
Centre for Marine Living Resources and Ecology, Kochi, Kerala, India.

*Correspondence e-mail: sanjeevanmoes@gmail.com

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Original Article

Abstract

Along the Kerala-Mangalore coast the peak spawning season of Indian mackerel coincides with the transition period from Spring Inter-monsoon to Summer Monsoon. The species spawn in the offshore waters (50 to 200 m isobaths) mostly in the South Zone and to a less extent in the North Zone. Mackerel mostly avoid the Central Zone for spawning and as nursery ground. Newly hatched larvae are 1.585 mm in standard Length (SL). Larval growth rates are significantly higher (0.339 mm D^{-1}) in the May-June spawning stock as compared to the July-August spawning stock (0.203 mm D^{-1}). Growth is allometric and involves the yolk-sac stage (1.49 mm to 2.84 mm SL), pre-flexion (1.80 mm to 3.3 mm SL), flexion (2.85 mm to 4.85 mm SL), and post-flexion (4.60 to 11.3 mm SL) stages. Mackerel larvae have only restricted swimming and manoeuvring abilities as their body depth is relatively higher, but have much better feeding abilities owing to their large mouth-gape. In the early stages of ontogeny, the larvae feed predominantly on microzooplankton and switch over to a diet dominated by Calanoid Copepods as they grow further. Main nursery grounds of mackerel larvae are located along the thermal fronts associated with cold-core eddies. Inter-annual variations in the abundance of mackerel larvae are influenced by the strength of winds that favour upwelling.

Keywords: *Mackerel larvae, upwelling, spawning, advection, flexion, turbulence, growth rate, eddies, surface currents, dispersion.*

Introduction

The Kerala-Mangalore coast is part of South Eastern Arabian Sea (SEAS), a typical Eastern Boundary Upwelling System (EBUS). Like other EBUS world over, the fishery of SEAS is dominated by small pelagic fish such as the oil-sardine (*Sardinella longiceps*), Indian mackerel (*Rastrelliger kanagurta*) and anchovies (*Stolephorus* spp.). Together they contribute as much as 49% of the fishery from this sector. Wide inter annual as well as decadal scale oscillations are observed in the catches of these species, the reasons for which are not yet fully understood. To large extent year-class strength is dependent on the growth and mortality rates associated with ontogeny, as explained by the match-mismatch hypothesis of Cushing (1975) and/or the stability hypothesis of Lasker (1985). Fish larvae are most susceptible during the transition from yolk-sac stage to the planktivorous stage (Lasker, 1975). Therefore, a clear understanding of the early life histories is a prerequisite in explaining the factors affecting recruitment and year–class strength in these species. The recruitment of marine fish populations having pelagic early life stages generally follow the optimal environmental window concept (Cury and Roy, 1989) or the triad processes (Bakun, 1996; Bakun *et al.*, 1998) of enrichment, concentration and retention. In the present context, enrichment and concentration correspond to upwelling areas and fronts respectively whereas retention is considered to be influenced by the offshore Ekman transport. Wind induced turbulence on the other hand act antagonistic to concentration process and is therefore detrimental to larval survival (Bakun *et al.*, 1998). Recruitment success and year-class strength are dependent on the productivity of the nursery grounds where the fish egg and larvae are retained. Though the oil-sardine, Indian mackerel and anchovies share the same ecological niche, subtle spatial and temporal variations in spawning and prey abundance in the preferred size spectrum are expected to be the key factors that determine recruitment success. Nevertheless, interspecific competitions can become a deciding factor in such years where aberrations in environmental cycles in the form of delayed onset of monsoon/ El-Nino events etc., may influence the spawning process of one or more related species. However, the present work is restricted to the ontogeny of Indian mackerel off the Kerala-Mangalore coast, without going to the complexities of interspecific competitions.

Indian mackerel exhibit relatively fast growth rates, attaining 190 mm by the end of the first year (Devaraj *et al.*, 1994) and reaching 200 to 220 mm by the second year (Sekharan, 1958). Length at maturity (L_m) ranges from 170 to 180 mm (Prathibha and Gupta, 2004; Sivadas *et al.*, 2006). Peak spawning season of Indian mackerel along the SW coast is May-June (Pradhan and Palekar, 1956; Noble, 1974; Yohannan and Abdurahiman, 1998) which corresponds to the initial phase of coastal upwelling in SEAS. Devaraj *et al.* (1997); Yohannan (1995) and Ganga (2010) reported on a single major brood originating sometime during February to May period and a secondary small brood that spawn in October- November. *Rastrelliger kanagurta* is a batch spawner (Pradhan, 1956; Yohannan, 1995) with determinate fecundity. Ganga (2010) noted that though *R. kanagurta* is a group synchronous batch spawner, the possibility of a secondary spawning occurring in the same season is remote and that most probably the unspent ova are degenerated or reabsorbed. There are wide gaps in the fecundity estimates of Indian mackerel. Antony Raja and Bandae (1972) estimated the fecundity as 37,200 eggs, Krishnakumar *et al.*, (2008) as 90,000 to 95,000 eggs whereas Ganga, (2010) is of the view that the fecundity in Indian mackerel ranges between 39,600 to 73,781 eggs with a relative fecundity of 476 ± 163 eggs.gm-1 body weight. In many fishes, final stages of gonadal development are dependent on energy reserves. However, in mackerels energy requirement for gonadal maturation are met by increased dietary intake and not depending on body reserves (Hasek and Felder, 2006). Yohannan (1995) and Ganga (2010) reported on rapid increase in feeding intensity in the 170-230 mm size groups of Indian mackerel, which is the length at which maturation is initiated and spawning activities predominate. Studies on the ontogeny of *R. kanagurta* from SEAS is limited to few descriptions on the occurrence and taxonomy by Balakrishnan (1957), Bennet (1967), Balakrishnan and Rao (1971), Silas (1974), Peter (1968), George (1988) and Binu (2003).

Material and methods

Study area

The study was carried out off the Kerala- Mangalore coast, along 9 pre-set transects extending from 30 m to 1000 m isobaths (Fig. 1). The study area form the southern sector of SEAS and is characterized by two dominant seasons, the Summer Monsoon (SM) from June to end September and the Winter Monsoon (WM) from November to end February interspaced by the Fall Inter Monsoon (FIM) in October and the Spring Inter Monsoon (SIM) from March to end May. In the present study, the Kerala-Mangalore coast is divided into three distinct zones namely the South Zone (SZ), Central Zone (CZ) and North Zone (NZ) on the basis of geological, physical and chemical attributes.

The south zone extends from Cape to Kollam (7° N-9° N), central zone from Kollam to Kozhikode (9° N- 11.5° N) and the north zone extends from Kozhikode to Mangalore (north of 11.5° N)

Sampling design

Ichthyoplankton surveys were undertaken on-board the Fishery Oceanographic Research Vessel (FORV) *Sagar Sampada* during the SM upwelling season of 2009, 2010 and 2013. Stations were selected along the Kerala-Mangalore coast extending

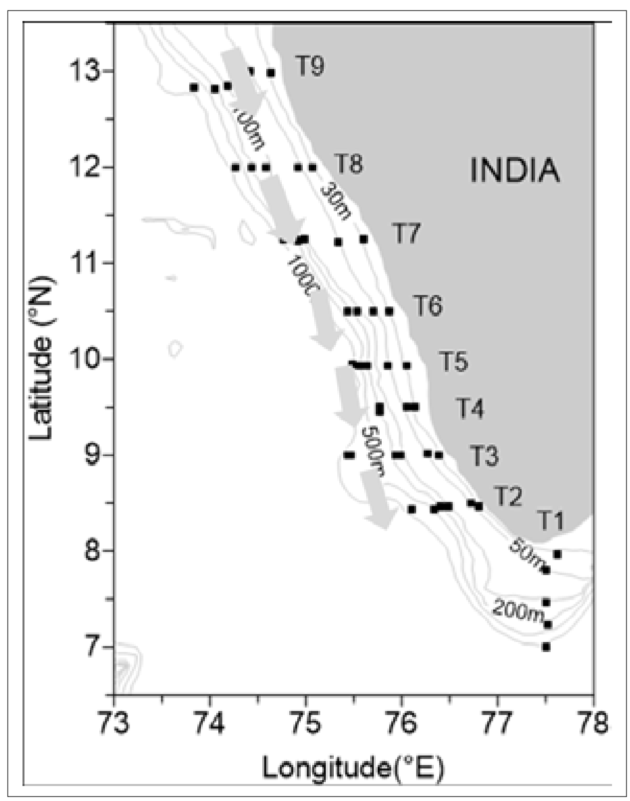

Fig. 1. Map showing study area and sampling sites along the transects off Cape (T_1), Thiruvananthapuram (T_2), Kollam (T_3), Alleppey (T_4), Kochi (T_5), Valappad (T_6), Kozhikode (T_7), Kannur (T_8) and Mangalore (T_9)

from 7.00°N to 13°N Lat. and 73.71° –77.64°E Long. covering 9 transects namely Cape – T_1 (8°N), Trivandrum – T_2 (8.5°N), Kollam - T_3 (9°N), Alleppey - T_4 (9.5°N), Kochi-T_5 (10°N), Valappad - T_6 (10.5°N), Kozhikode -T_7 (11.2°N), Kannur–T_8 (12°N) and Mangalore T_9 (13°N). Horizontal collections of ichthyoplankton were taken from a total of 172 stations representing the 30m, 50 m, 100 m, 200 m, 500 m and 1000 m isobaths.

Data collection

Data collections were made covering the different phases of summer monsoon such as the onset phase of 2009 (29-05-09 to 14-06-09) and 2010 (07-06-10 to 14-06-10, peak phase of 2009 (4-08-09 to 20-08-09), 2010 (15-06-10 to 08-07-10) and 2013 (15-07-13 to 14-08-13) and late phase of 2009 (18-09-09 to 1-10-09). Surface ichthyoplankton collections were made by horizontal towing of paired Hydro Bios Bongo Net (300 microns mesh) equipped with a digital flow meter for 10 minutes at a constant vessel speed of 2 knots. Mesozooplankton samples from mixed layer were collected by vertical haul using Multiple Plankton Net (MPN) of Hydro Bios (mesh size of 200 μm and mouth area 0.25 m^2). After the estimation of biomass by displacement volume method, mesozooplankton samples were preserved in 4 % buffered formalin. Mackerel eggs collected from spawning grounds were reared in the automated aquarium on-board at 26°C.

Oceanographic parameters were collected from each station by using Sea Bird 911 plus Conductivity, Temperature and Depth sensor (CTD) fitted with 12 litre Niskin bottles. Sea Surface Temperature (SST) was measured using bucket thermometer. Chlorophyll-a was estimated spectrophotometrically using Perkin Elmer U-V Visible Spectrophotometer following the 90% acetone extraction method (Parsons *et al.*, 1984). Meteorological observations on wind speed, direction, humidity, air temperature, atmospheric pressure etc. were recorded in 15 minutes interval along the track using the IRAWS on-board. Additional oceanographic/ meteorological data to support the study were obtained from FORV Data Centre and/or derived from North Indian Ocean Atlas (NIOA) by Chatterjee *et al.* (2012). Continuous profiling of currents was done up to 500 m in 4m /8m bin using the RDI hull mounted broadband (76.5 KHz) Acoustic Doppler Current Profiler (ADCP). Surface geostrophic currents estimated from Sea surface height values (JASON-1) and climatological mean dynamic height and processed by the NRL site at the Stennis Space Center are taken from NOAA coast watch portal.

Data Analysis

The entire sample were sorted and counted for qualitative and quantitative analysis of micro and mesozooplankton. Mackerel larvae were identified up to species level under Leica S8 APO trinocular stereomicroscope following the taxonomic descriptions by Peter (1968) and Silas (1974) and assigned with developmental stages such as yolk sac, pre-flexion, flexion and post-flexion stages following Kendall (1984) and Lalithambika (1986). Larval abundance is represented as ind.10 m^{-2} area (Smith and Richardson, 1977) by multiplying the volume of water filtered with the Mixed Layer Depth (MLD). In the laboratory, the mesozooplankton samples were sorted to taxonomic groups according to ICES, 1947; Newell and Newell, 1973; Todd and Laverack, 1991 and standardised to ind.10 m^{-2}. Photographs as well as measurements were taken under Leica DFC 425 Image viewer.

Results

During the present study period mackerel eggs were recorded on 2.6.2009 from the 50 m station (975 eggs per 10 m^2) and the 200 m station (255 eggs per 10 m^2) off the Trivandrum transect and on 11.6.09 from the 50 m station (530 eggs per 10 m^2) and the 100 m station (1180 eggs per 10 m^2) off the Kannur transect. From the 172 Bongo operations carried out during the study period, only on 29 occasions (16.86%) one or more mackerel larvae could be obtained in the samples. Of the 4850 mackerel larvae collected, 67.98% were from the 50 m, 14.82% from the 100 m, 13.96% from the 200 m and 2.31% from the 500 m isobaths (Table 1). The 30 m depth contour accounted for only 0.58% of the larvae collected. An offshore station located at 1450 m depth off Cape yielded 7 mackerel larvae in the bongo collections made on 15.07.2013. Fig. 2 shows the distributional pattern of mackerel larvae along the Kerala-Mangalore coast during the SM upwelling season. South and North Zones accounted for 89.24% and 9.88% respectively in the larval abundance, whereas larval abundance in the Central Zone was only 0.88% (Table 2). Maximum larval abundance was in the first half of June (92.33%), followed by the second half of May (4.60%) and the rest during first half of July (0.76%), second half

Table 1. Percentage occurrence of mackerel larvae within the MLD of isobath

Station Depth (m)	Total No. of stations sampled	Number of positive stations	% of positive stations	Number of larvae (in 10 m^2)	% occurrence
30	37	2	5.41	28	0.58
50	42	9	21.43	3297	67.98
75	1	1		10	0.21
100	33	7	21.21	719	14.82
200	37	8	21.62	677	13.96
500	7	1	14.28	112	2.31
750	1	0	0	0	0
1000 & above	14	1	7.14	7	0.14
Total	172	29	16.86	4850	100

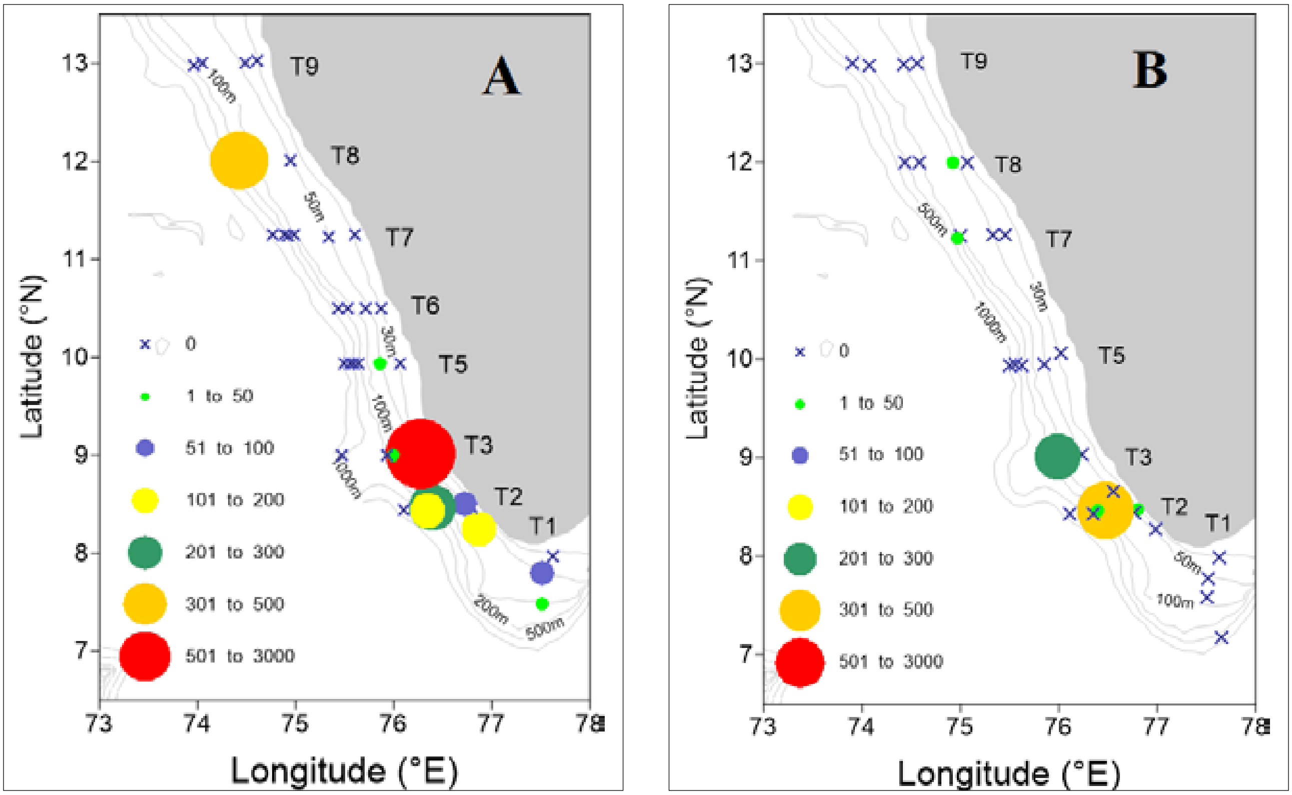

Fig. 2. Distribution and abundance of mackerel larvae during (A) initial phase of SM 2009 and (B) initial phase of SM 2010

of July (0.87%) and the first half of August (1.44%)). Like most planktonic forms, the mackerel larvae showed distinct dial migrations. Mean larval density (number of larvae per 10 m^2) in the bongo collections were maximum during the first half of night (111) followed by the second half of the night (13.8), dusk (8), first half of day (8), dawn (4) and second half of the day (1.7).

Developmental Stages

Morphological features of the mackerel egg, yolk-sac stage, pre flexion, flexion and post flexion stages of the larvae as observed under stereo zoom microscope are given below:

Table 2. Numerical abundance of mackerel larvae in different geographical zones. Parenthesis gives % contribution

Month	South Zone	Central Zone	North Zone	Total
Last half May	223	0	0	223(4.60%)
First half June	4088	2	388	4478(92.33%)
Second half June	-	-	-	-
First half July	-	-	37	37(0.76%)
Second half July	17	25	-	42(0.87%)
First half August	-	16	54	70(1.44%)
Total	4328 (89.24%)	43 (0.88%)	479(9.88%)	4850 (100%)

Egg:- Egg of *Rastrelliger kanagurta* is pelagic and spherical with a smooth chorion. Egg measure 0.91 to 0.98 mm in diameter and contain a single large oil globule, 0.23 to 0.25 mm in diameter. Fertilized eggs are transparent with a clear perivitelline space (Fig. 3a). In newly fertilized eggs, cell division starts opposite to the vegetal pole. Cleavage of cell leads to the formation of a blastodermal cap. Germinal ring develops as a small band at one pole. With the development of embryonic axis, the embryo becomes more distinct (Fig. 3b). At this stage, the development of head and outline of optic vesicles are distinguishable. Pigment spots appear on the body contour.

Yolk-sac stage:- Larvae measure 1.49 mm to 2.84 mm in standard Length (SL). The newly hatched larva has a curled shape with a distinct yolk sac on its anterio-ventral side (Fig. 3c). The larva has 24-25 myomeres which are not very distinct. The ventral side of the body has 18 melanophores. Eyes are not pigmented. In the field collections, few larvae measuring above 3 mm SL still retained reduced yolk sac.

Pre Flexion stage:- Body moderately built and measure between 1.8 and 3.3 mm SL. Alimentary canal is coiled and extends up to 48% SL. Posterior part of gut protrudes out. The larvae are devoid of pre opercular spines. Dorsal and anal rays are not distinct, but seen as a continuous fin fold (Fig. 3d). Of the

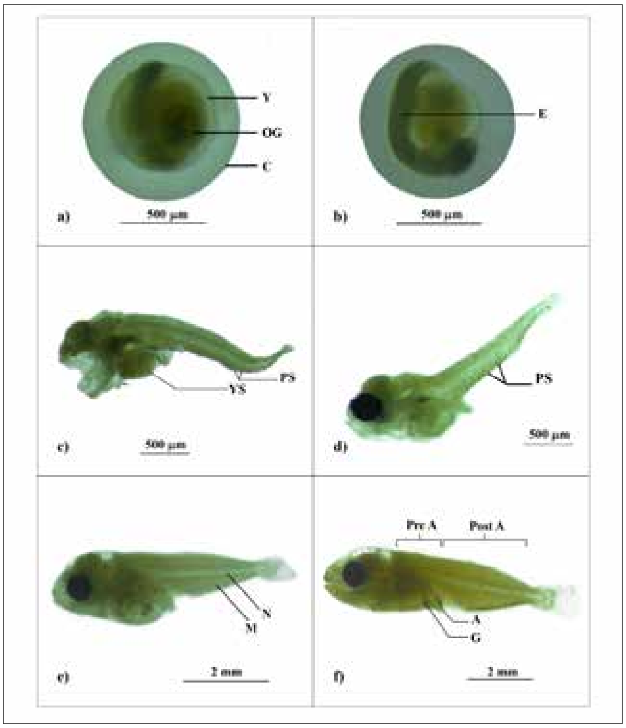

Fig. 3. Developmental stages of Indian mackerel. (a) Middle stage egg (b) Late stage egg (c) Yolk sac larva (d) Pre flexion larva (e) Flexion larva (f) Post flexion larva. [Y – Yolk; OG – Oil Globule; C – Chorion; E – Embryo; YS – Yolk sac; PS – Pigment spots; M – Myomere; N – Notochord; G – Gut; A – Anus; Pre A – Pre anal; Post A – Post Anal]

30 myomeres present, 7 are pre anal and 23 are post anal. Though mouth opening is visible, mouth lacks teeth. The ventral margin of the body has 19 melanophores and dorsal margin is not pigmented. Melanophores are absent on occipital region. A single melanophore on urostyle and two pigment spots on the side of gut base.

Flexion stage:- Larva measure 2.85 to 4.85 mm in SL. Alimentary canal is coiled, compact and forms 49% of SL. Of the 30 myomeres that are clearly visible, 7 are pre anal and 23 are post anal. The notochord flexion starts from 2.85 mm SL. Rays are not distinct and clear. Pelvic fin not developed (Fig. 3e). Teeth start to appear at 4.1 mm SL. Melanophores are present on the ventral margin of the body (15), lower base of caudal peduncle (2), occipital region (2) and side of gut (3 to 4).

Post Flexion stage:- SL range from 4.6 to 11.3 mm (11.3 mm larvae represent the largest specimen in the present study). Body laterally compressed with moderate body depth. Body is deeper at the head and gut than the tail. Gut triangular shaped and coiled. Alimentary canal extends up to 54% of the SL. Teeth present both on the upper and lower jaw. Pre-opercular spines absent. First dorsal with 8 spines and second dorsal with 12 soft rays. 12 anal soft rays present. Dorsal and anal finlets 6 each and 12 -13 caudal rays present. Pelvic fin-buds appear in specimens above 8 mm SL. Stellate pigments (13-14) on occipital region. Melanophores on tip of upper jaw (4) cleithral opercular region (4), lower cleithral region (1) and posterior to jaw (1). 4 of the pigments are present on the lower base of caudal fin and 2 on mid of caudal peduncle at the angle of flexion. Dorsal pigmentation develops as the larvae reaches post flexion stage. 15 melanophores present on the dorsal fin base from middle of body to caudal peduncle. 3 melanophores present on side of gut. 12 - 13 melanophores on the ventral margin of the body (Fig. 3f).

Numerical abundance (in 10 m^2 area) of mackerel larvae in the pre flexion, flexion and post flexion stages within the 3 geographic zones during different phases of SM is given in Table 3.

Larval growth rates

Newly hatched mackerel larvae (4 numbers) reared in aquarium tanks on-board FORV-SS measured between 1.49 mm and 1.78 mm SL and survived only for two days. The relationship between the SL and egg size could not be established for fear of damaging the eggs while taking egg diameter measurements. Growth curves fitted on larval frequency modes show significant difference in the growth pattern of larvae from May-June and July-August spawning stocks ($p < 0.05$). F-test gives a value of 2.775 with P as 0.00076 between the two variables. Larvae from May-June spawning stock grow much faster ($Y = 0.339 X + 2.3004$) than the larvae from July-August spawners ($Y = 0.204 X + 1.7155$). On hatching, the larvae from both the spawning stocks were almost of the same length (1.5 & 1.54 mm SL), but after the first week of growth, larvae from the May-June batch reached 4.75 mm SL, whereas those from the July-August batch were only 3.13 mm SL. At the end of the second, third and fourth week the variations in larval length (SL in mm) were 7.56 & 4.84, 9.55 & 5.98 and

Table 3. Developmental stages of mackerel larvae (ind.10 m^{-2} area) and their % contribution (in parenthesis) in the 3 zones during different phases of SM season

Phase of SM	South Zone			Central Zone			North Zone			
	Pre F	F	Post F	Pre F	F	Post F	Pre F	F	Post F	Total
15 May to 14 June	1179 (25.08)	2185 (46.48)	947 (20.14)	0	1 (0.02)	1 (0.02)	28 (0.60)	360 (7.66)	0	4701 (96.93)
15 June to 14 July	9 (19.57)	0	0	0	0	0	9 (19.57)	28 (60.86)	0	46 (0.95)
15 July to 14 Aug.	7 (6.8)	0	1 (0.97)	22 (21.36)	3 (2.91)	16 (15.53)	11 (10.68)	37 (35.92)	6 (5.83)	103 (2.12)
Total										4850

11.3 & 7.2 mm SL respectively (Fig. 4). Mackerel larvae exhibit allometric growth of body parts. Regression of variables such as Head Length (HL), greatest Body Depth (BD) and Lower Jaw Length (LJL) on SL of mackerel larvae gave coefficients of 0.311X for HL, 0.2817X for BD and 0.1056X for LJL. Comparison of the HL, BD and LJL of mackerel and oil sardine larvae coexisting in the same habitats show that the proportion of HL to SL in mackerel larvae is significantly higher in comparison to oil-sardine (Fig. 5a). The same is true for BD (Fig. 5b) and LJL (Fig. 5c).

Environmental set up

Starting from May to end September, SEAS is under the grip of SM, characterized by strong surface waves, associated turbulence and moderate to intense coastal upwelling. Signatures of coastal upwelling such as fall in SST and Mixed Layer Depth (MLD), increase in Sea Surface Salinity (SSS) and productivity (Table 4) are evident in the South zone in May itself and extend to the northern zones as the season progresses. Surface winds drive a relatively strong southward flowing West India Coastal Current (WICC) oriented close to the coast along the northern

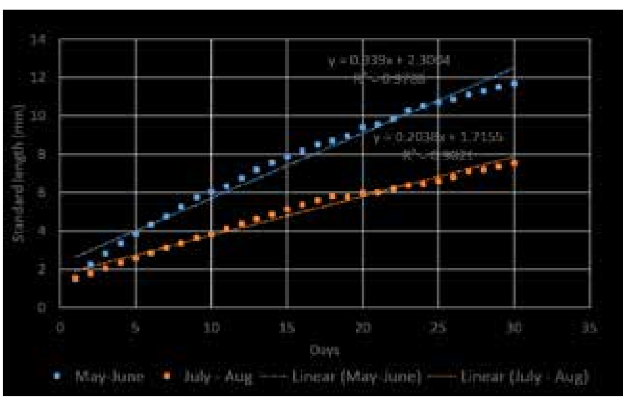

Fig.4. Growth rate of *Rastrelliger kanagurta* larvae from May- June and July-August breeding stocks

parts of SEAS, the distance between the coast and the current widening south of 11.5°N. In the area between the WICC and the coast of SZ, the winds and surface currents are irregular and changes direction at short intervals giving rise to several small eddies (Fig. 6) that are transient in nature and lack coherence. Surface currents are directed equator-ward up to 11.5° N and are irregular south of 11.5° N. Wind induced turbulent energy is quite high and several areas of high turbulence (W3 > 250) are distinguishable (Table 5). Except for few pockets of high larval abundance (> 100 larvae per 10m²), overall larval density was low, probably due to the dispersal of larvae under intense turbulent conditions. These pockets of larval abundance correspond to the thermal fronts (Table 6). Analysis of MPN data indicates that the vertical distribution of mackerel larvae is restricted to the mixed layer above the thermocline. Though mackerel larvae were obtained in the present study from areas

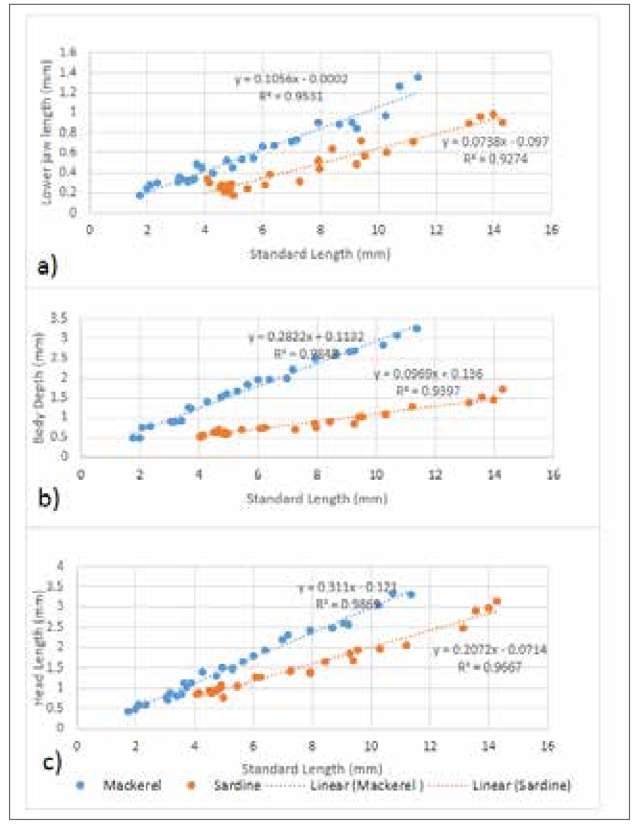

Fig. 5.Comparison of mackerel and oil-sardine larval morphology: (A) LJL on SL (B) BD on SL and (C) HL on SL

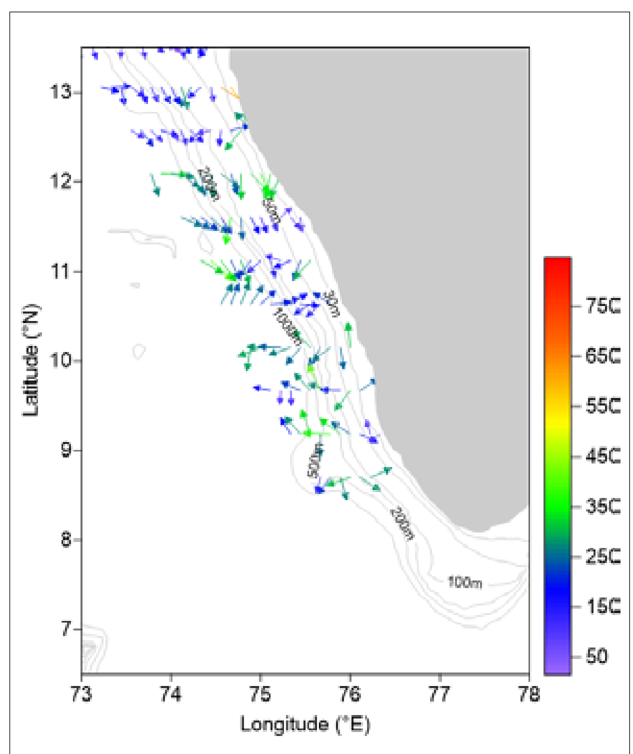

Fig.6. Surface currents (at 16m level) derived from ADCP

Table 4. Monthly average of Environmental conditions and Productivity. (Number of observations in each month is given in brackets along with the average and range values for each variable)

Zone	Month	SST(°C)	SSS	S-DO (ml/L)	MLD (m)	Chl-a (mg/m3)	Zooplankton	
							MZP (indm-2)	MesoZP(ml.m-3)
South Zone	May(10)	25.86	35.01	4.84	10.4	11.91	34375	1.91
		24.83-27.03	24.89-35.21	3.43- 6.42	6-21	6.48-22.75	23750-46250	0.11-3.81
7° N to	June(25)	26.65	35.02	4.32	14.12	2.04	71944	3.14
9° N		24.97-29.44	34.27-35.44	2.62-6.08	6-38	0.08-8.89	5000-138125	0.46-13.33
	July(9)	25.47	34.92	4.01	14.67	2.04	18400	1.67
		23.93-26.49	34.71-36.26	3.09-5.50	10-23	0.30 -5.98	15200-21600	0.8-3.6
	August(14)	24.80 23.05-27.77	34.98 34.49-35.26	3.67 1.67-5.82	16.92 6-34	10.50 3.50-24.94	2.56 0.24-13.33	
Central Zone	May (10)	31.01	34.32	4.45	15	0.12		0.27
		30.71-31.35	33.78-34.68	4.14-4.68	8-23	0.05-0.38		0.02-0.47
9° N to	June (21)	28.54	35.14	4.52	15.38	2.42		1.07
11.5° N		26.37-29.56	34.41-35.56	3.18-6.27	6-34	0.25-8.98		0.1-3.27
	July (12)	26.06	32.99	3.89	10.83	2.39	19600	1.49
		24.40-28.30	31.61-33.77	2.58-5.16	6-23	0.65-7.60	15200-24000	0.004-3.5
	August (14)	26.44	33.08	3.87	8.14	1.84		2.19
		25.13-28.56	31.60-34.95	2.60-4.60	6-20	0.56-5.77		0.5-2.75
North Zone	May (12	31.2	34.67	4.36	23.8	0.208		0.295
		31.04-31.36	34.46-34.73	4.1-4.7	20-30	0.03-0.62		0.018-0.66
11.5° N	June (12)	28.92	35.17	4.01	13.25	1.14		1.04
to 13°N		28.58-29.59	34.47-35.72	3.21-4.87	6-33	0.09-3.39		0.67-1.5
	July (12)	28.42	34.90	4.99	15.5	0.37		0.47
		28.07-28.80	34.52-35.36	4.52-5.56	6-24	0.10-0.50		0.004-1.3
	August (21)	27.05	33.83	3.74	11.8	1.73	25100	1.76
		23.59-28.57	31.71-35.56	1.47-5.01	6-36	0.04-5.85	8400-52400	0.4-5.92

with wide range of SST (23.81 to 29.59°C), SSS (31.61 to 36.34) and DO level (2.60 to 6.29 ml/L), it appears that the optimum/ preferred range of conditions are SST in the range of 26.20 to 27.75°C (~ 60% larval abundance), SSS in the range of 34.5 to 35.5 (~ 60% larval abundance) and DO above 3 ml/L (93% abundance).

Discussion

From the present study, it is evident that the peak spawning season of Indian mackerel coincides with the SIM to SM transition period that falls in the second half of May in SZ and the first half of June in NZ. These results are consistent with the observations of Pradhan and Palekar (1956), Noble (1974), Yohannan (1995), Devaraj *et al.* (1997), Yohannan and Abdurahiman (1998) and Ganga (2010). However, the present observations are restricted to the period mid-May to mid-August (upwelling season) and therefore the possibility of spawning during March–April (Krishnakumar *et al.*, 2008) or October – November (Ganga, 2010), could not be established. It is known that fish stocks release its larvae into the annual production cycle at the best time to secure food (Cushing, 1975) and the right environmental conditions (Lasker, 1981) to ensure good survival (Cury and Roy, 1989). Indian mackerels are believed to be microzooplankton feeders in their critical stage of ontogeny (Madhupratap *et al.*, 1994) whereas more advanced mackerel larvae feed predominantly on calanoid copepods (Arthur, 1976; Ostergaard *et al.*, 2005). Arthur (1976) noted that jack mackerel larvae first starts to feed when they are 3.25 mm long on a diet predominantly composed of small copepod adults (55.6%) followed by tintinnids (13.7%) and copepod nauplii (12.8%) and that the larvae perceive food organisms by their colour. SIM season in SEAS is characterized by good sunlight, weak winds (av. 3.7m s^{-1}), strong surface stratification (shallow MLD), high surface DO levels and oligotrophic conditions that promote the spread of microbial food web of pico/ nano autotrophs and microzooplankton (Table 4) dominated by ciliates and heterotrophic dinoflagellates (Asha Devi *et al.*, 2010). With the onset of upwelling season (SM) in June, winds become strong (turbulent conditions), eutrophic conditions prevail especially in the coastal waters and the microbial food-web is replaced within few weeks by the conventional food-web of diatoms (Lathika *et al.*, 2013) and copepods which form >80% of the mesozooplankton abundance (Asha Devi *et al.*, 2010).

Table 5. Influence of wind, offshore Ekman drift and turbulence on the distribution of mackerel larvae

Transect	Depth (m)	Distance (Km)	Date	Mackere Larvae (ind.m^{-2})	Wind speed ($m.s^{-1}$)	W^3 index $m3s^{-3}$	Ekman drift ($cm.s^{-1}$)	Wind Direction (°)
Cape	30	18.85	31.5.09	0	4.19	73.56	2.72	12
	50	31.64	31.5.09	53	5.26	145.53	22.94	17
7° N	100	67.04	30.5.09	21	6.03	219.26	0.93	346
	1450	77.73	15.7.13	7	2.1	9.26	0.55	346
TVM	30	1.98	31.5.09	0	1.99	7.88	1.30	347
		5.16	7.6.10	23	6.52	277.17	34.17	72
	50	15.12	2.6.09	79	1.99	7.88	2.44	74
8° N	60	20.17	31.5.09	149	4.25	76.77	0.33	359
	100	37.24	2.6.09	10	1.16	1.56	0.54	79
		48.84	9.6.10	377	4.39	84.60	1.84	86
	200	44.64	2.6.09	211	2.23	11.09	4.05	223
		57.64	9.6.10	44	3.51	43.24	0.005	208
		53.1	16.7.13	1	3.11	30.08	6.50	134
	500	67.29	1.6.09	112	4.79	109.90	3.32	349
Kollam	30	13.33	3.6.09	0	5.73	188.13	12.36	324
9° N	50	27.34	3.6.09	2935	6.64	292.75	1.89	331
	100	57.47	4.6.09	33	6.66	295.41	30.38	329
		57.36	14.6.10	264	1.99	7.88	1.24	148
Alleppey	30	18.52	19.7.13	0	3.22	33.39	1.92	140
	50	29.62	19.7.13	0	0.76	0.44	0.13	291
9.50° N	100	60.99	19.7.13	0	2.94	25.41	0.43	199
	200	60.55	19.7.13	5	2.79	21.72	2.34	196
Kochi	30	19.33	14.6.09	0	4.75	107.17	12.17	201
	50	42.56	13.6.09	2	1.88	6.64	2.25	213
10° N		43.44	8.8.09	3			5.92	357
	100	62.25	30.7.13	13	1.09	1.30	0.012	318
	200	70.48	8.8.09	12 6	4.48	89.92	8.25	343
		74.18	31.7.13		0.94	0.82	0.12	30
Vallapad	30	18.7	12.6.09	0	7.69	454.76	1.19	328
	50	35.01	12.6.09	0	4.54	93.58	9.79	310
10.50° N	100	54.93	12.6.09	0 1	2.61	17.78	0.02	303
	115	52.53	2.8.13				0.73	319
Kozhikode	30	16.93	9.6.09	0	3.42	40.00	8.28	10
	50	50.09	7.8.09	8	4.82	111.98	15.59	4
11.25° N	100	84.50	10.6.09	0	3.45	41.06	1.28	322
	200	91.48	8.6.09	0	4.61	97.97	3.33	328
		88.72	3.7.10	10			11.39	322
Kannur	30	13.25	11.6.09	0	4.19	73.56	0.22	312
	50	31.12	6.8.09	41 27			21.43	357
12° N		35.48	6.7.10				0.05	183
	100	64.05	11.6.09	0	6.09	225.87	23.35	301
	200	83.24	12.6.09	386	4.43	86.94	2.88	281
Mangalore	30	17.46	4.8.09	5			3.23	322
	50	34.83	29.6.09	0	1.39	2.69	0.75	186
13°N	100	80.32	29.6.09	0	1.14	1.48	0.002	155
	200	91.40	29.6.09	0	1.16	1.56	0.07	278

Table 6. Environmental set up of Larval retention areas

Transect & dates	Depth (m)	Larval abundance (ind.10 m^2)	SST (C)	SSS	Density	Ekman drift (cm s^{-1})	W^3 index m^3. s^{-3}	Chl mg.m^{-3}
Trivandrum								
31.5.2009	30	0	25.36	35.21	23.39	1.30	26	22.75
31.5.2009	50	149	26.38	35.01	22.92	0.33	77	8.89
2. 6. 2009	100	10	26.38	35.01	22.92	0.54	2	4.56
2.6.2009	200	211	26.87	35.41	23.06	4.05	11	1.05
1.6.2009	500	112	29.19	34.89	21.92	3.32	110	0.36
7.6.2010	30	23	25.22	34.27	22.73	34.17	277	1.38
7.6.2010	50	0	24.97	34.78	23.18	15.92	362	0.93
9.6.2010	100	377	26.45	34.92	22.83	1.84	85	4.31
9.6.2010	200	44	27.27	35.21	22.78	0.01	43	1.23
Kollam								
3.6.2009	30	0	27.26	34.97	22.61	12.36	188	2.27
3.6.2009	50	2935	27.76	34.94	22.42	1.89	293	1.10
4.6.2009	100	33	29.22	35.13	22.09	30.38	295	4.66
16.6.2010	30	0	26.23	34.30	22.43	4.61	23	6.70
16.6.2010	50	0	26.37	35.54	22.57	4.61	25	8.98
14.6.2010	100	264	26.97	34.92	22.67	1.24	8	8.55
Kannur								
11.6.2009	30	0	28.58	35.42	22.52	0.22	74	2.85
11.6.2009	50	0	28.98	35.02	22.09	0.85	113	0.39
11.6.2009	100	0	29.08	35.47	22.39	23.35	226	3.39
12.6.2009	200	386	29.59	35.72	22.41	2.88	87	0.65

It appears that the Indian mackerel have adjusted their main spawning season to coincide with the transition period from late SIM (mid-May) to SM (mid-June), when food availability and the environmental conditions are most favourable to ensure fast growth and survival of their larvae. This is evident from the fact that, in the present study the larval growth of the July-August spawning stock was found significantly lower ($P < 0.00076$) compared to the May-June spawning stock.

Mackerel eggs were collected from off the Trivandrum from 50 m (975 eggs per 10m^2) and 200 m (255 eggs per 10m^2) stations on 2.6.2009 and from the off Kannur 50 m (530 eggs per 10m^2) and 100 m (1180 eggs per 10m^2) stations on 11.6.2009. At Trivandrum in 30 to the 50 m depth strata the estimated Ekman drift is only 1.30 cm s^{-1} which works out to a possible 1.12 km D^{-1} offshore transport of eggs and for the 100 m to 200 m depth strata with an Ekman drift of 0.54 cm s^{-1}, the maximum offshore transport can only be 0.47 km D^{-1}. Similarly for the Kannur transect, the offshore transport can only be 0.19 km D^{-1} at the 50m station and 0.73 km D^{-1} at the 100 m station. The fact that high concentrations of eggs (least dispersal) were obtained in all the collections together with the relatively weak offshore transport of eggs, indicate that the Indian mackerel spawn in the surface waters (MLD) between the 50 m and 200 m depth contours. Oliver (1990) have also reported that the main spawning grounds of Cape horse-mackerel in the northern Benguela region are coincident with its nursery grounds located between 100 m and 300 m isobaths and that the planktonic stages did not undergo substantial drift.

Despite the good concentration of eggs in the spawning grounds, larval abundance was relatively low except for few pockets of abundance corresponding to thermal fronts with almost all Bongo collections represented by pre flexion, flexion and post-flexion stages in varying proportions. This indicates to the wide dispersal of larvae due to the strong turbulent conditions existing during the SM season. When wind-speed exceeds 4 ms^{-1}, which is sufficient for occasional wave-breaking to begin, turbulence is created and the rate of dissipation is enhanced (Thorpe, 2007). Turbulent energy is roughly proportional to the cube of wind-speed (W^3 index). Laskar (1985); Peterman and Bradford (1987) provide evidence that turbulence in the euphotic layer increases larval mortality during the critical period of ontogeny. Spawning grounds of many clupeid fishes are generally located where the seasonal average W^3 index does not exceed 250 $m^3 s^{-3}$ values (Bakun *et al.*, 1998). However, during the entire SIM season, surface waters especially of the SZ are highly stratified due to the presence of low saline Bay of Bengal waters (Vinayachandran *et al.*, 2007; Sabu and Ravichandran, 2011; Rao *et al.*, 2014), which prevents breakdown of water column stability by wind action and therefore provide less turbulent conditions. By adjusting their peak spawning season to May – June, larvae and juveniles of Indian mackerel are exposed to less environmental risks and therefore the mackerel fishery of the west coast is relatively steady in comparison to the oil-sardine fishery which show wide inter-annual and decadal scale oscillations (Krishnakumar *et al.*, 2008).

Among the three geographical zones, the SZ accounted for 89.24% of the mackerel larvae collected and the NZ 9.88%. Collections were close to nil (0.88%) in the CZ despite near even sampling efforts at the three zones. Off the Kochi coast, Noble (1974), noted a general dominance of juveniles only and very few mature mackerel in commercial landings. Ganga (2010) reported large scale occurrence/ migration of juvenile mackerel to the CZ during the period immediately following the monsoon. It appears that mackerel avoid the CZ for spawning and as nursery ground, perhaps due to the existence of SM mud-banks along this coast which makes it difficult for the young larvae to search food by colour vision. Grinson *et al.* (2013) reported that the 'Chakara fishery' (mud-bank fishery) of CZ is dominated by egg-bearing oil-Sardine (51.2%), *Stolephorus* spp. (16.7%) and shrimps (15.68%) whereas the Indian mackerel formed only 2.14% in the fishery. Another possible reason for avoidance of CZ by mackerel may be the strong off shore advection which may transport the larvae to far-off locations where enrichment is poor and larval mortality will be high. Haugen *et al.* (2002) have reported that the maximum off-shore extent of the upwelling process is recorded in the Kollam–Kochi region of CZ. On the basis of *in-situ* observations (CTD) and estimated upsloping (from wind stress) of 24° isotherm, Smitha *et al.* (2008) established that off-shore transport at SZ is purely wind driven whereas in areas north of this, the offshore transport is mediated through the combined effect of wind stress and off-shore propagating Rossby waves radiating from the upwelling mode of the pole-ward moving coastally trapped Kelvin waves (Amol *et al.*, 2012). In the CZ this off-shore advection is maximum as the equator ward flowing WICC carrying Arabian Sea High saline Water (ASHSW) that limit the offshore extent of the advection is far off the coast in comparison to the northern region where the WICC is much closer to the coast .

Larval rearing experiments on-board FORV-SS though not fully successful, showed that newly hatched mackerel larvae on an average are 1.585 mm in SL (range 1.49 to 1.78 mm SL). Growth rates of larvae estimated from growth curves of the May-June and July-August brood stocks were found significantly different, being 0.339 mm D^{-1} and 0.203 mm D^{-1} respectively. Though we could not establish the relation between egg size and length of the newly hatched larvae, it is well known that the greater size of larvae from larger eggs positively influence growth and survival (Brooks *et al.*, 1997; Kalmer, 2005). Intraspecific variations in egg size and its ecological implications have been reported by Ware (1975). Nevertheless, in our study, the larger larvae (as estimated from growth curve) hatched from the July-August brood stock attained lesser growth rate which implies that food availability rather than the size of the newly hatched larvae are more important in determining growth and survival.

Mackerel larvae show allometric growth, as is evident from the regression of HL, BD and LJL on SL. Studies by Ostergaard *et al.* (2005) and Bachiller and Irigoien (2013) also show that most fish larvae grow in an allometric fashion. Morphology of fish larvae is of prime importance in the process of prey search and capture. Swimming and manoeuvring abilities of the larvae are dependent on body depth (BD), whereas mouth gape (LJL) determines the maximum size of prey the larvae is able to ingest (Lasker, 1981). Compared to the oil-sardines the swimming and manoeuvring abilities of Indian mackerel are rather restricted by their greater BD. This is more than offset by a larger mouth gape (LJL) which permits them prey on food items of wide size range. In the case of Jack mackerel larvae, Arthur (1976) noted that they can ingest particles three times larger in diameter than can sardine larvae of same length and that during development the larvae invade new niches (of prey size) with preference on Calanoid copepods. Therefore competition with smaller sized larvae for smaller sized prey is lessened (Munk, 1992). It appears that early larval stages of Indian mackerel thrive on the microzooplankton especially small copepods and ciliates that are abundant (251 ± 155 X 10^{-3} ind.m^{-2}) during SIM and onset SM (First half of June) and as the larvae grow in size, they switch over to mesozooplankton especially the copepods that are abundant (245 ± 293 ml 100 m^{-3}) during peak SM (Asha Devi *et al.*, 2010).

During the initial phase of SM 2009, mackerel larvae were abundant in the offshore areas off Trivandrum (T_2), Kollam (T_3) and Kannur (T_8) transects whereas during the same period of 2010 larval abundance was much less. Mackerel larvae appear in the CZ only during the peak phase of SM, probably when the mud-banks dissipate. ADCP measurements show that the surface currents are equator-ward up to 11.5° N. South of this the surface currents are irregular. This is due to the presence of mesoscale cold-core eddy/ies (associated with Lakshadweep Low) in the SZ from the beginning of SM season, which propagate north-westward as the season progresses and dissipate by the end of the season (Shankar and Shetye, 1997; Haugen *et al.*, 2002; Jineesh *et al.*, 2015). In the eddy region the equatorward WICC flow west of the eddy and therefore the area between the coast and the WICC is quite extensive, unlike the NZ where the WICC is closely oriented to the coast. This area is characterized by the presence of several small scale eddies that are transient in nature and supplement the SM upwelling to enhance the overall productivity of the area. Frontal zones (thermal fronts) associated with these cold core eddies, seems to be the main spawning and nursery grounds of Indian mackerel implying that the processes of enrichment, concentration and retention play significant roles in larval survival and recruitment success. Similar observations on the role of mesoscale eddies on ichthyoplankton assemblage in the Gulf of Alaska is reported by Atwood *et al.* (2010). It is well established that upwelling along the SZ is forced primarily by SM winds that flow tangential to the coast (Bakun *et al.*, 1998; Smitha *et al.*, 2008). During the 2010 SM upwelling season, the winds off the SZ were relatively weak which might have resulted in below average upwelling and poor larval growth and survival. The observation of Rao *et al.* (2014) that for the period 1998 to 2010 the Arabian Sea Warm pool was most pronounced during 1998, 2003 and 2010 supports this view.

Subtle variations in mackerel spawning grounds, spawning season, nursery ground, larval morphology and food preferences in the early stages of ontogeny to a great extent reduces interspecific competition with larvae of oil-sardine and anchovies that coexists with mackerel larvae. Recruitment anomalies in mackerels is therefore more dependent on the environmental set up of the spawning and nursery grounds rather than over exploitation of the stock (Krishnakumar *et al.*, 2008).

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