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ORIGINAL ARTICLE

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ABSTRACT

Near reef abundance and coast–offshore distribution of tuna larvae around Minicoy Island were studied based on three cruises carried out on board FORV *Sagar Sampada* during 2014–15. The samples were collected by oblique tows using bongo twin nets (300 micron) for three seasons (Fall inter-monsoon (FIM), Spring inter-monsoon (SIM) and Summer monsoon (SM)) in six on–offshore stations ranging from 1 to 20 km off-shore of the Minicoy. Results indicated that the tuna larvae aggregate in the near reef waters and total tuna larvae abundance (all the species combined) shows a decreasing trend towards off-shore. Tuna larvae are found to be more abundant during SM and FIM. Comparison of the species-wise variation in tuna larvae for one season (SM) indicated that the larvae of *Euthunnus affinis* (32.5%) dominated among the tuna species, followed by *Auxis* spp. (31.6%), *Thunnus* spp. (3.9%) and *Katsuwonus pelamis* (2.7%). A pattern of highest larvae abundance in the near reef areas was observed except for *Thunnus* larvae. GAM indicated that mean seawater temperature and mean seawater salinity are the major environmental factors that significantly influence the larvae abundance, particularly for *Thunnus* followed by *Katsuwonus pelamis*, *E. affinis* and *Auxis* spp. The study confirms that the environmental parameters show high variation between stations and among transects as a result of the complex oceanographic characteristics around the islands. Further studies with better understanding of the larvae dynamics and their association with the environmental parameters including physical processes are essential to elucidate these relationships more clearly.

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Introduction

The marine fisheries sector is considered an important source of occupation and livelihood for at least 3 million people in over 3600 fishing villages along the Indian coastline (Anon 2006). The average annual yield from the marine capture fishery of India in recent years is ∼3.5 million tons from ∼200 species of commercially important fin fishes and shellfish (Pillai and Pillai 2000; Anon 2015; Nair 2015).

The Lakshadweep group of islands (08°00′N–12°30′N, 71°00′E–74°00′E) consist of 11 inhabited and 25 uninhabited islands, scattered in the Arabian Sea about 200–400 km west off the Malabar coast. The region undergoes seasonal reversals in wind pattern according to the summer and winter monsoons, and the prevailing oceanographic processes and water-mass structures are modified according to the seasonal forcing (Shanker et al., 1997). The region experiences a lowering of sealevel in response to the presence of a cyclonic gyre, resulting in enhanced (though not significant) production and thinning of the mixed layer (or shallowing of thermocline) during the summer monsoon (June–September). The prevailing process is exactly the opposite during spring (March–May). A deep thermocline, shallow mixed layer (due to stratification), presence of a barrier layer and very high temperatures (>29°C) at the surface level associated with less nutrients and biological production are the peculiarity of the seasons (Sabu and Revichandran, 2011). Tunas (Family Scombridae) are well represented in Indian waters, and several species of tunas and mackerels contribute to the country's commercial and recreational fisheries (Pillai et al. 2002; Rohit et al. 2011; Kumar et al. 2015). Large pelagic species such as tunas and other tuna-like species are more abundant in the oceanic island territories of the Indian Exclusive Economic Zone (EEZ) (Theivasigamani and Subbiah 2014; Karuppasamy 2016). *Katsuwonus pelamis* (skipjack tuna), *Thunnus albacares* (yellowfin tuna), *Auxis thazard* (frigate tuna) and *Euthynnus affinis* (little tunny) are the

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major tuna species mainly caught from Lakshadweep waters (Kumar et al. 2015). The estimated total marine fish catch from Lakshadweep in 2014–2015 was 12,185 t of which tunas constituted 92% (11,231 t) (CMFRI 2015). Among tunas, *K. pelamis* (68%) was the most important species landed, followed by *T. albacare* (25.7%), *E. affinis* (4.5%), *A. thazard* (1%) and *Gymnosarda unicolor* (0.4%) respectively (CMFRI 2015).

The information available on the life history and distribution of early larval stages of scombroid fishes from Indian waters is limited to coastal waters (Balakrishnan, 1957; Jones and Kumaran 1964; Peter 1968, 1977, 1982; Balakrishnan and Narayana Rao 1971; Silas 1974; George 1979, 1989; George 1988; Binu 2003). Tunas are highly migratory, efficient predators of the epipelagic realm, and are assumed to complete their life cycles in the open ocean (Pillai and Ganga 1985; Pillai et al. 2002; Pillai and Satheeshkumar 2012, 2014). Tunas such as *T. albacares* and *K. pelamis* are generally considered as archetypal oceanic species (Sund et al. 1981; Reglero et al. 2014) and studies on the larval stages of these oceanic tunas in the Indian waters are scanty. Based on this assumption, most of the studies on tuna larvae in the world oceans are restricted to oceanic waters (Fowler et al. 2008; Chen et al. 2014; Laiz-Carrión et al. 2015; Dominigues et al. 2016; Cornic et al. 2018). However, previous studies confirmed that larval abundance of these fishes are higher in near coral reefs (Leis 1993; Fowler et al. 2008).

The distribution of tuna larvae, particularly of the commercially important genera *Thunnus* and *Katsuwonus*, needs to be extensively investigated to identify their spawning grounds and to estimate the spawning stock biomass from the larval surveys (Scott et al. 1993; Schaefer 2001; Chen et al. 2014; Laiz-Carrión et al. 2015; Domingues et al. 2016). Surveys carried out in the oceanic waters of the Pacific Ocean reported high tuna larvae concentrations in the near reef areas (Leis et al. 1986).

Nearly all the sampling for tuna larvae has been conducted in the upper ocean in view of the current understanding of the oceanic distribution (depth of migration) of adults. However relatively high concentrations of tuna larvae have been reported from previously under-sampled tropical areas near reef locations (Miller 1979; Leis et al. 1986; Boehlert and Mundy 1994). The abundance of *T. albacares* and *K. pelamis* larvae was found to be higher in near reef waters compared with offshore waters (Miller 1979), which was later confirmed by Fowler et al. (2008) and Leis et al. (1986), irrespective of the seasons. However, contrary to these results, Matsumoto et al. (1984) reported offshore spawning behaviour in *K. pelamis*. All these results show variations in the spawning pattern of these large pelagic tunas in the world oceans (Matsumoto 1958, 1966). Members of the coastal tuna genus *Auxis* are also diverse in their preference for spawning grounds/seasons and oceanographic characteristics (Uchida 1981a, 1981b; Boehlert and Mundy 1994). Near reef areas have not received much attention in the studies of distribution and abundance of tuna and billfishes. Therefore, larval abundance surveys that do not include these areas may underestimate their abundance. Further studies are required to confirm the generality of this hypothesis.

Oceanographic features such as temperature, salinity, depth/topography, turbidity, turbulence and productivity strongly influence the abundance of fish larvae, as confirmed by various authors (Harris et al. 1999, 2001; Garcia et al. 2005; Wexler et al. 2011; Alvarez et al. 2015; Cornic and Rooker 2018; Puspasari et al. 2018). Further, the influence of mesoscale hydrodynamic features such as fronts, gyres and eddies on the spawning behaviour of tunas has been well documented in many studies (Rodriguez et al. 2013; Garcia et al. 2005; Reglero et al. 2014; Alvarez et al. 2015; Cornic and Roorker 2018). Eddies and frontal areas are reported to harbour abundant tuna larvae as these are areas of convergence and retention which support high zooplankton abundance (Bakun, 2006; Satoh 2010; Cornic and Roorker 2018). The onset phase of the monsoon season is reported to significantly influence spatial distributional patterns in fish larval assemblages as it is strongly linked with water current dynamics and upwelling processes that promote nutrient enrichment and food availability (Hsieh et al. 2011a, 2011b). The physicochemical attributes of the nursery grounds strongly influence the growth and survival of tuna larvae, as confirmed by many studies (Garcia et al. 2013; Kim et al. 2015; Cornic and Rooker 2018), and are indicators for predicting the spawning stock biomass of tunas (Scott et al. 1993; Hsieh et al. 2006; Ingram et al. 2017). The present study is an effort to gather information on the environmental factors associated with the larval habitats and to delineate the key factors that influence the recruitment success in tuna fishery of Lakshadweep waters. Tuna being a trans-oceanic group, detailed studies at a regional scale on the distribution and abundance of the larvae are critical to the judicious utilization of these resources. The major objectives of this study are (1) to check any discernible pattern of coast–offshore and near reef variations in tuna larval abundance in the waters around the Minicoy Island; (2) to understand the seasonal variation in the larval abundance; and (3) to delineate the key environmental factors influencing the abundance and distribution of tuna larvae species using GAMs (generalized additive models) based on presence/absence data.

Materials and methods

Data and samples used in the present study were collected through three dedicated cruises of the Fishery Oceanographic Research Vessel (FORV) *Sagar Sampada* during Fall inter-monsoon (FIM) (Cr.330, 16.10.2014–22.10.2014), Spring inter-monsoon (SIM) (Cr.338, 13.04.2015–18.04.2015) and Summer Monsoon (SM) (Cr.342 21.07.2015–27.07.15) around Minicoy Island in the Lakshadweep Sea. The focus of the study was on the distribution of fish larvae with special emphasis on the family Scombridae. Details of the sampling locations are given in Figure 1. Six transects were surveyed around the island with each transect having six stations from near reef waters to offshore waters (Figure 1).

Plankton samples were collected using Bongo twin nets with mesh size of 300 µm and ring diameter of 60 cm. A digital flow meter was centrally mounted at the mouth of one of the nets to determine the volume of water filtered. The filtering cone of the net was 250 cm in length to which a collecting bucket was fitted. A 20 kg hydrodynamically shaped cast metal depressor was mounted to the ring to keep the equilibrium of the net during the tow. Samples were taken from each of the six stations along a transect located at 1, 3, 5, 10, 15 and 20 km away from the outer reef crest of the island. However, we could not sample three locations each in the third and fourth transects during cruise no. 342 due to unfavourable weather conditions. Oblique tows from 100 m to surface were carried out since the tuna larvae distribution is known to vary with depth (Tim et al. 1990). All the six stations in one transect were sampled in one day. Transects 1, 2 and 3 are considered as windward and 4, 5 and 6 are leeward transects for the comparative analysis. All tows were operated during daylight, between one hour after sunrise and one hour before sunset.

Samples were preserved onboard in 4% buffered formalin in filtered seawater immediately after estimating the total as well as fish larvae biomass separately. For detailed analysis, samples were brought back to the CMLRE lab. The environmental parameters were recorded by Sea Bird CTD 911 plus equipped with temperature, conductivity and pressure sensors.

The fish eggs and larvae were sorted out from the entire sample for quantitative and qualitative analysis at the CMLRE lab using a stereo-zoom microscope (Leica MZ 16). For uniformity in quantification, the tuna larvae abundance was standardized to number of larvae/10 m^3 of the volume of water filtered during hauling (Goswami 2004; Harris et al. 2000).

Tuna larvae, to the extent possible were identified up to species level, following standard identification keys (Fritzscher 1978; Nishikawa and Rimmer 1987) using 10–115× magnifications using Leica S8 APO trinocular stereomicroscope and Leica MZ 16 stereomicroscope. Identification of *K. pelamis* was carried out following the description given by Matsumoto (1958). Larvae of *Thunnus*, *Auxis* and *Euthynnus* were identified following Richards and Potthoff (1974) and Matsumoto (1959). We used morphological characteristics and pigment patterns of the tuna larvae for the species identification.

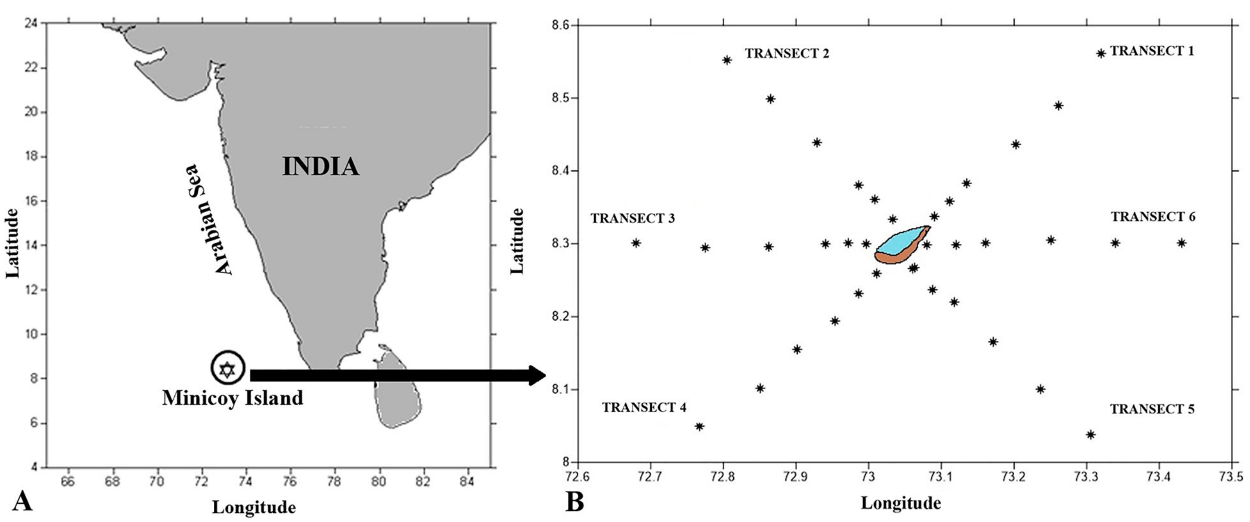

Figure 1. Sampling stations around Minicoy Islands in Lakshadweep Sea, India. Map shows the area of the study (A) and the six transects and 36 stations selected for the sample collections (B).

Osteological characters were also attempted for the larval identification rather than relying solely on pigments especially for the identification of *Thunnus* larvae following Richards et al. (1990). However, pigment patterns and morphology were the major characteristics considered for the identification. Nearly 29.3% of tuna larvae could not be considered for the analysis due to uncertainties in identification.

Statistical analysis

The presence of the tuna larvae is represented as larval abundance (larvae/10 m^3) (Harris et al. 2000; Goswami 2004). We used two sets of data for the comparative analysis. The first data set used comprehensive tuna larval abundance for seasons combined whereas the second data set considered only one sampling period (cruise no. 342). Here tuna larvae were categorized into four groups, viz. *E. affinis*, *Auxis* spp., *K. pelamis* and *Thunnus* spp.

Statistical analysis of horizontal distributional patterns of total tuna larvae were performed on log-transformed values (log10) after checking normality and homoscedasticity of the samples (Shapiro–Wilk and Levin's tests). A count of 1 was added to all the values before transforming the data to eliminate zero values that exist in the data (zero tuna larvae was reported only from one station). A two-factor ANOVA was performed to evaluate the possible influence of sampling period on spatial distribution of tuna larvae. The coastal–off shore and near reef abundance of fish larvae were compared using two-factor ANOVA. We also tried to understand any significant difference in totals between windward and leeward stations using two-factor ANOVA. Pair-wise differences among the stations were analysed using Tukey's HSD (post-hoc analysis) if the ANOVA showed a significant difference ($P < 0.05$).

Further, a principal component analysis (PCA) was performed based on the correlation matrix of the oceanographic variables to understand their effect on the tuna larvae abundance (Sebates 1990; Tondato et al. 2010; Rabbaniha et al. 2014; Álvarez et al. 2015). We derived two environmental parameters, viz. the mean values of seawater temperature and seawater salinity (0–90 m) as the samples were collected during oblique haul, apart from the parameters recorded using CTD. A total of seven environmental parameters (sea surface temperature (SST), mean seawater temperature (0–90 m) (MSWT), sea surface salinity (SSS), mean seawater salinity (0–90 m) (MSWS), turbidity, density and oxygen) were considered for the PCA analysis.

To test the hypothesis that tuna species abundance varies with major environmental variables and distance away from the island, we used a GAM (generalized additive model) to predict the presence or absence of different species of tuna larvae in the study area (Maravelias and Reid 1997; Murase et al. 2009; Perryman and Babcock 2017). GAM is a non-parametric multiple regression method that helps to model a response (dependent) variable as a function of one or more predictor (independent) variables which also address the non-linear relationship between dependent and independent variables using a non-parametric smoother (Hastie and Tibshirani 1990; Yee and Mitchell 1991; Doyle et al. 2009; Auth et al. 2011). Here we have used a second set of data for the analysis, which contains a large number of zero values in the species-level fish larvae data (*Thunnus* spp., 25 nos; *K. pelamis*, 28 nos; *E. affinis*, 23 nos; *Auxis* spp., 17 nos). Hence, we used a GAM binomial approach (Fox et al., 2000; Zuur et al. 2009; Auth et al. 2011; Ohshimo et al. 2017). Linear regression is found to be ineffective in the majority of the cases since the dependent variable (tuna larvae abundance) does not have a linear relationship with the environmental variables, as observed in previous studies (Austin 1999; Young and Carr 2015). Sea surface temperature, mean seawater temperature (0–90 m), sea surface salinity and mean seawater salinity (0–90 m) were the major environmental parameters selected for the model, along with a non-environmental parameter, distance (km). This variable (distance) was expected to give a better understanding about any coast–offshore variation in the tuna larvae abundance, if it exists. We removed the parameters such as oxygen, turbidity and density from the models as they do not show any significant relationship with the larval abundance.

We performed GAM analysis for each species separately using a forward selection approach to examine the effect of various environmental variables on the larvae abundance since the number of observations restricts us from adding more than two environmental variables at a time to the model (Polourde et al. 2014). GAMs are widely used in the modelling of species distributions to predict the relationship between species abundance and environmental parameters (Doyle et al. 2009; Murase et al. 2009; Young and Carr 2015). We have calculated 'Deviance explained' (which is analogous to the variance in a linear regression), GCV (Generalized Cross Validation Criterion) and adjusted R^2 to assess the robustness and predictability of the model. GCV is interpreted as the AIC (Akaike Information Criterion) which is the measure of fit and parsimony of the models (Doyle et al. 2009; Murase et al. 2009;

Rooker et al. 2012). The best model is selected based on the gain in deviance explained and low GCV scores.

Model descriptions

We analysed the presence of tuna larvae under the assumption that

$$Y_i \cong \text{Bin}\,(1,\ \pi_i), \tag{1}$$

$$\text{var}(Y_i) = \pi_i \times (1 - \pi_i), \tag{2}$$

$$\text{logit}(\pi_i) \cong \alpha + \text{factor}\,(\text{Sta}) + s(\text{env.var1}) + s(\text{env.var2}) \tag{3}$$

where Y_i is the response variable for the presence/absence of different species of tuna in the transect $_i$. The parameters π_i and Bin indicate the probability of the presence of larva in the sample and the binomial error, respectively. α, Sta, env.var1 and env.var2 indicate a constant, sampling station, environmental variable 1 and environmental variable 2, respectively. *Factor*() indicates factor descriptors, and *s*() indicates numerical descriptors processed with smoothing splines.

All the statistical analysis was carried out using R version 3.0.2 (R Foundation for Statistical Computing, Vienna) and PAST (PAlaeontologicalSTatistics, version. v1.81) (Hammer et al., 2001). Significance level was set at 0.05 for all statistical tests used. The GAM models were performed using the R package mgcv in the R version 3.0.2 (R Foundation for Statistical Computing, Vienna). Function *s* used in the model is a thin-plate regression spline fitted to the environmental parameter used.

Results

Over 1000 fish larvae were caught during the sampling. Bothidae, Acanthuridae and Scombridae are some of the major families observed during the study. The tuna larvae abundance of the six transects during three different seasons is shown in Table I.

Table I. Summary on the number (mean and SD) tuna larvae collected from Minicoy Island in Lakshadweep Sea during 2014–15.

Season	Distance (km)	Mean and SD of number of tuna larvae	Mean and SD of tuna larvae abundance (nos/10 m^3)
Fall inter-monsoon	1	19.167 ± 3.430	2.210 ± 0.842
	3	11.333 ± 4.633	1.077 ± 0.364
	5	12 ± 1.265	0.863 ± 0.195
	10	7 ± 3.578	0.722 ± 0.502
	15	6.5 ± 1.975	0.487 ± 0.125
	20	3.833 ± 2.041	0.312 ± 0.166
Spring inter-monsoon	1	25.667 ± 4.131	1.938 ± 0.400
	3	15.167 ± 3.371	1.599 ± 0.824
	5	14.167 ± 3.970	0.895 ± 0.367
	10	12.667 ± 5.317	0.798 ± 0.403
	15	7.833 ± 3.970	0.450 ± 0.262
	20	5.667 ± 2.875	0.372 ± 0.202
Summer monsoon	1	21.6 ± 3.912	3.261 ± 1.121
	3	13 ± 4.123	1.783 ± 0.656
	5	12.3 ± 5.785	1.081 ± 0.648
	10	13.4 ± 4.099	0.885 ± 0.420
	15	8.8 ± 3.834	0.472 ± 0.259
	20	6.33 ± 2.503	0.402 ± 0.179

SD, Standard Deviation.

The results indicated that the tuna larvae aggregated in the near reef waters (ANOVA, $P < 0.05$). There was a significant reduction in tuna larvae abundance from the near shore waters which extends up to 5 km away from the island. There is a statistically significant difference in tuna larvae abundance between seasons (ANOVA, $P < 0.05$). A significant difference was noticed in the tuna larvae abundance between SM and FIM. Tuna larvae were found to be abundant during SM and SIM compared with FIM (Tukey's HSD, $P < 0.05$). Within this, higher abundance of tuna larvae was observed during SM compared with SIM; however, these variations are statistically not significant. Also, a significant difference was observed in the larvae abundance in the first three stations compared with the three offshore stations (1–5 km) (Figure 2) (Tukey's HSD, $P < 0.05$).

Our observations indicated a pattern of high tuna larvae abundance in the windward compared with leeward side irrespective of season. However, this pattern was more pronounced during SIM compared with SM. No such variation was evident during FIM.

We did a comparative analysis to understand the variations in abundance of different tuna larvae (*Thunnus* spp., *K. pelamis*, *E. affinis* and *Auxis* spp.) (second data set). We identified the larvae of two tuna species up to species level (*K. pelamis* and *E. affinis*) and two species up to genus level (*Thunnus* and *Auxis*). There was a significant difference in the abundance of different tuna larvae when all stations were combined (ANOVA, $P < 0.05$), dominated by *E. affinis*, *Auxis* spp., followed by *Thunnus* spp. and *K. pelamis* (Tukey's HSD, $P < 0.05$). The abundance of *E. affinis* larvae was high among tuna species from the area (Table II), followed *by Auxis* spp., *Thunnus* spp. and *K. pelamis* (Tukey's HSD, $P < 0.05$). The larvae of skipjack tuna were found to be the lowest among the tuna species (Tukey's HSD, $P < 0.05$), with 0.07 no./10 m^3 reported from both near reef as well as offshore waters. However, the difference between the larval abundance of *K. pelamis* and *Thunnus* spp. was not statistically significant. We observed in general that tuna larvae of early or preflexion stages were mainly reported from the stations which are close to

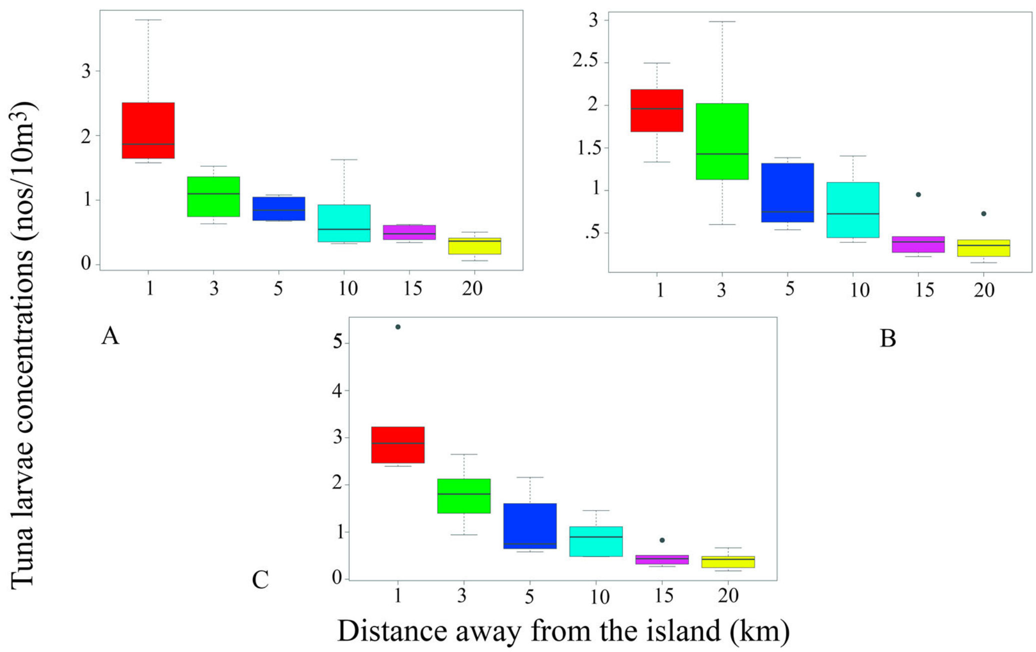

Figure 2. On–offshore and near reef concentration of tuna larvae around Minicoy Island in the Lakshadweep Sea during 2014–2015 (three seasons combined).

the island. Fish larvae in more advanced stages were observed from the offshore waters.

The environmental parameters are found to be highly varying among the six transects surveyed with distance (Figure 3). However, this pattern was not clear for transects 3 and 4 since we were able to survey only three stations in these transects due to unfavourable weather conditions. We have not attempted to compare the oceanographic conditions of these transects as it may give unrealistic comparisons, hence, we restricted our comparisons to only four transects (1, 2, 5, 6). Transects 5 and 6 reported high sea surface temperature and low sea surface salinity compared with the other transects. Sea surface salinity showed a negative relationship with distance for three transects (1, 5, 6), while transect 2 showed a positive relation. In transect 6, mean sea surface temperature was found to increase with distance whereas mean sea surface salinity showed a declining trend. For transect 5, unlike SST, mean seawater temperature declines with distance. Mean sea surface salinity showed a declining trend with distance except for transects 1 and 2. Oxygen concentration pattern was also highly varied between stations with distance which showed a declining and increasing trend for transect 1 and 6, respectively. No clear pattern was observed for turbidity. However, transect 5 and 6 showed a declining trend up to 10 km and changed thereafter. Water density also varied significantly between transects. Highest and lowest densities were recorded for transect 1 and transect 6, respectively. However, it failed to show any significant pattern except for transect 2 which showed a decreasing trend with distance.

PCA clearly differentiated the three seasons based on the oceanographic parameters considered. The first five PC axes indicated 98.4% of the total variation. PC 1 and 2 show nearly 81.6% of the total variations (66.8 and 14.9% of the variations, respectively). Differentiation in the first axis is mainly contributed by density ($r = 0.43$), mean salinity ($r = 0.42$), SST ($r = -0.41$), surface salinity ($r = 0.42$) and oxygen ($r = -0.37$). Turbidity ($r = 0.74$) and distance ($r = -6.44$) were the major environmental parameters responsible for the variation in axis 2. This

Table II. Summary of the on-off shore distribution of different species of tuna larvae around Minicoy Island, Lakshadweep Sea during July 2015.

Species	The mean and standard deviation of tuna larvae abundance (nos/10 m^3) at different stations away from the island					
	1 km	3 km	5 km	10 km	15 km	20 km
E. affinis	0.159 ± 0.120	0.100 ± 0.032	0.156 ± 0.063	0.058 ± 0.017	0.108 ± 0.098	0.086 ± 0.034
K. pelamis	0.072 ± 0.016	0.069 ± 0.017	0.055 ± 0.019	0.064 ± 0.016	0.068 ± 0.016	0.063 ± 0.006
Auxis sp	0.111 ± 0.031	0.106 ± 0.041	0.182 ± 0.062	0.079 ± 0.019	0.090 ± 0.021	0.077 ± 0.015
Thunnus sp	0.066 ± 0.005	0.090 ± 0.060	0.111 ± 0.102	0.072 ± 0.009	0.111 ± 0.076	0.063 ± 0.006

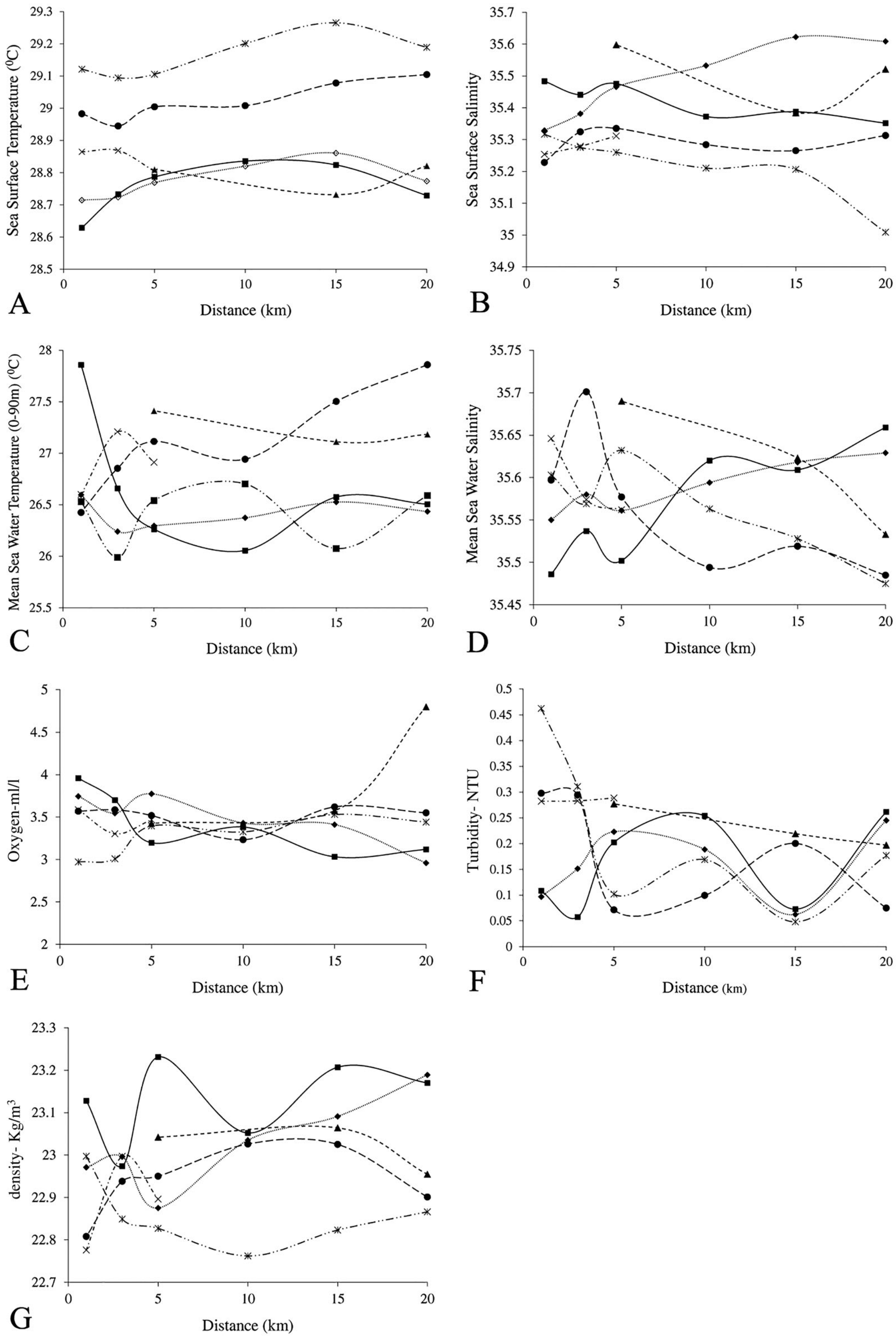

Figure. 3. Variations in the environmental parameters with respect to the distance for all the transects surveyed around Minicoy Island in the Lakshadweep Sea.

clearly indicates that the environmental parameters considered for the analysis are very different during the three seasons. PCA clearly differentiated FIM and SIM which occupy the positive and negative values in axis 1. Whereas, SM falls in an intermediate position between the other two seasons (FIM and SIM). However, SM falls closer to FIM than SIM. Salinity and density are found to be high in FIM, whereas SIM is characterized with high temperature and oxygen. We made a 2D bubble plot superimposed on the PCA plot to understand the variation of total fish larvae and tuna larvae abundance during the three seasons and the influence of major oceanographic parameters on their abundance. The bubble plot superimposed on the PCA indicated that total fish larvae abundance failed to establish any significant pattern of coast–offshore distribution (Figure 4). The 2D bubble plot shows a pattern of near reef abundance of tunas during SM; tuna larvae abundance was found to be high in SM. The abundance of tuna larvae was high in near reef waters, which are more turbid, than the offshore areas. During SM, the mean values of all oceanographic parameters studied (sea surface temperature, mean seawater temperature (0–90 m), sea surface salinity, mean seawater salinity (0–90), density (0–90 m), oxygen (0–90 m) and turbidity (0–90 m)) were in an intermediate position compared with the other two seasons (Table III).

GAM showed a significant negative relationship between distance from shore and tuna larvae abundance (adj. R^2, 0.678; deviance explained, 78.2; GCV, 0.5957, $P < 0.0001$) (Figure 5A). However, it failed to show any species-specific effect. GAM also indicated significant correlations between larvae abundance and various environmental variables for all the four species of tuna studied (Figure 5A–H). The abundance of *Thunnus* spp. showed strong relationships with mean seawater temperature (0–90 m) and mean seawater salinity (0–90 m) (Figure 5B–C). However, sea surface temperature and sea surface salinity give better predictions for *K. pelamis* and *E. affinis* (Figure 5D, F, G). Sea surface temperature and mean surface salinity were found to give strong predictions for *Auxis* species (Figure 5H). Tuna larvae abundance showed a non-linear relationship with environmental parameters except for *K. pelamis*. Mean seawater salinity showed a positive linear relationship for *K. pelamis* larvae abundance (Figure 5E). The abundance of *Thunnus* spp. was found to fluctuate with mean seawater temperature

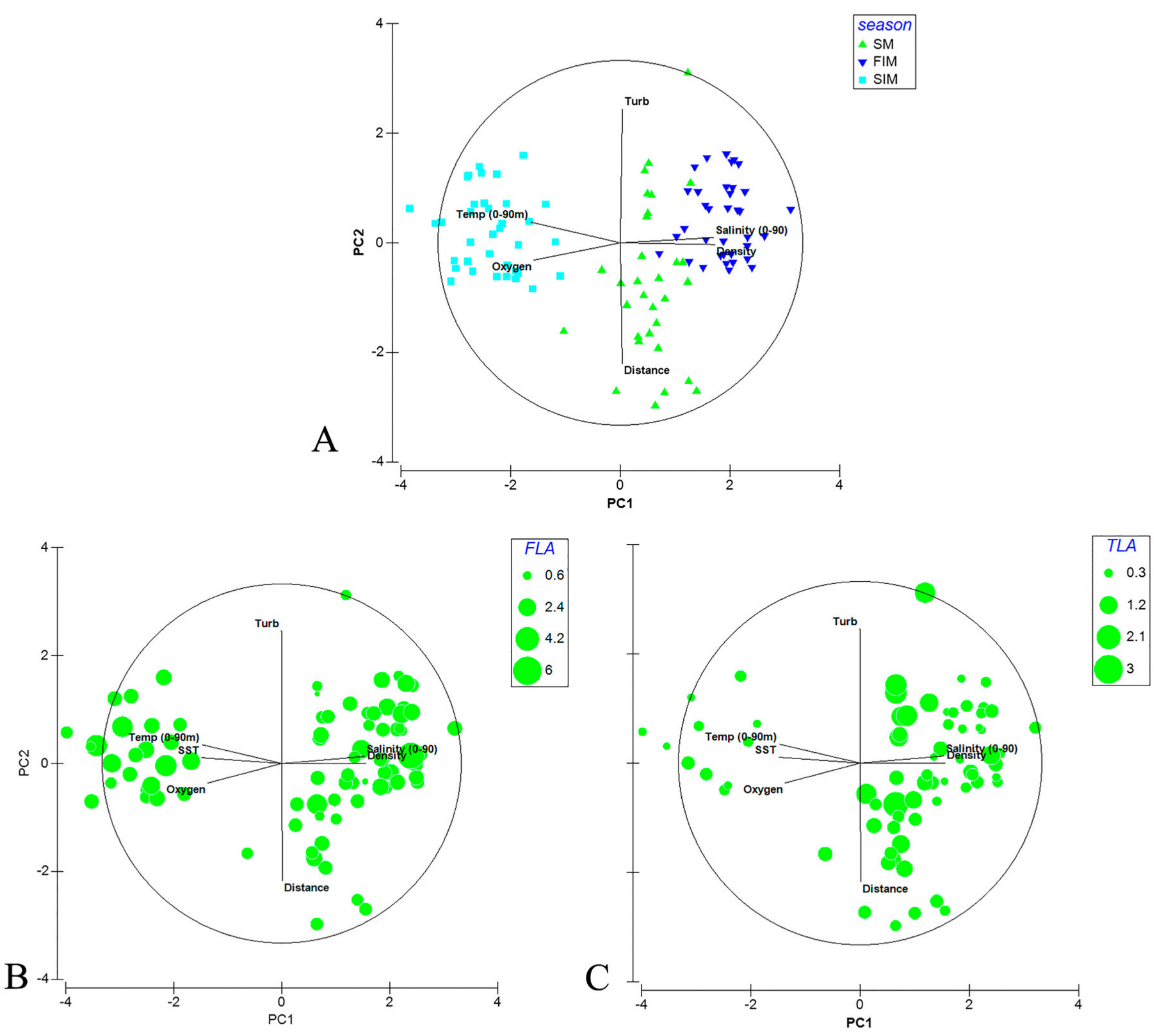

Figure 4. Bubble plot superimposed on the PCA showing the relationship between total fish larvae (B) and tuna larvae abundance (C) with various environmental parameters during three cruises conducted around Minicoy Island in the Lakshadweep Sea during 2014–2015.

Table III. Summary of various environmental parameters recorded around Minicoy Island in Lakshadweep Sea during 2014–2015.

	Sea Surface Temperature °C		Mean Sea Surface Temperature °C (0–90 m)		Sea Surface Salinity		Mean Sea Surface Salinity (0–90 m)	
Seasons	Min-Max	Mean ± SD	Min-Max	Mean ± SD	Min-Max	Mean ± SD	Min-Max	Mean ± SD
SM	28.54–29.27	28.89 ± 0.18	25.99–27.86	26.73 ± 0.49	34.32–35.62	35.29 ± 0.29	35.48–35.72	35.58 ± 0.06
FIM	28.89–29.27	29.03 ± 0.11	25.99–27.86	26.67 ± 0.42	35.29–36.21	35.73 ± 0.19	36.04–36.96	36.17 ± 0.15
SIM	30.26–30.88	34.53 ± 0.15	26.68–29.8	29.07 ± 0.48	33.54–34.27	33.88 ± 0.19	33.96–35.17	34.61 ± 0.26
	Density (0–90 m)		Oxygen (0–90 m)		Turbidity			
	Min-Max	Mean ± SD	Min-Max	Mean ± SD	Min-Max	Mean ± SD		
SM	22.55–23.23	22.96 ± 0.15	2.96–4.8	3.50 ± 0.38	0.05–0.46	0.20 ± 0.10		
FIM	23.27–23.84	23.65 ± 0.12	2.65–3.65	3.08 ± 0.24	0.28–0.30	0.29 ± 0.01		
SIM	21.01–22.1	21.72 ± 0.26	3.20–4.32	4.01 ± 0.28	0.25–0.29	0.27 ± 0.01		

(Figure 5B), being highest at 26.75–27°C and declining thereafter. However, it showed a negative correlation with mean seawater salinity (Figure 5C). The relationship between *K. pelamis*, *E. affinis* and *Auxis* spp. abundance with SST is found to be non-linear and shows a negative relationship with SST (Figure 5D, F, H), following a similar pattern. Abundance of *E. affinis* larvae was found to increase with SSS (Figure 5G). The deviance explained by the GAM ranges from 78.9–37.5, 81.3–35.5, 75.7–53 and 67.8–52.2 for *Thunnus* spp., *K. pelamis*, *E. affinis* and *Auxis* spp., respectively (Table IV).

Discussion

The Lakshadweep Islands are well known for their rich tuna resources and their economy completely depends upon this fishery (Kumar 2014; Kumar et al. 2015). A better understanding of the spatial and temporal distribution of fish larvae, especially tuna, is very important for the conservation as well as sustainable management of resources. The present study is the first attempt to understand the near reef and coast–offshore distributions of tuna larvae and their relationship with major environmental parameters, around the Minicoy Island in Lakshadweep Sea, India. Our study observed that total tuna larvae abundance was significantly higher in the near reef stations compared with the offshore areas, which is in accordance with previous studies in other waters (Miller et al. 1979; Leis et al. 1986; Leis 1993; Fowler et al. 2008; Rodriguez et al. 2013). We observed that tuna larvae abundance was progressively decreasing up to a distance of 5 km away from the island, with no significant difference thereafter, which confirms the near reef effect. This is agrees well with earlier findings (Miller 1979; Leis et al. 1986; Leis 1993; Fowler et al. 2008) of high larvae abundance in near reef waters up to 5 km away from the reef. This pattern was found to be consistent among the three seasons for all tuna larvae, indicating that near reef larval distributions persist over seasonal time scales, as reported by previous studies (Leis 1993; Fowler et al. 2008).

The tuna larvae abundance in the near reef areas was found to be high during the summer monsoon compared with the other two seasons. The surface runoff during the monsoon period is responsible for the high productivity in the near reef waters which can enhance the larval food availability (Devi 1999; Lo et al. 2010; Torres et al. 2011). Conand and Richards (1982) reported high abundance of *T. albacares* and *K. pelamis* larvae in the Madagascar region (Indian Ocean) during the summer season. However, there are several studies which were not in agreement with these findings, indicating that tuna larvae prefer to stay near to the reef, irrespective of season (Miller et al. 1979; Leis et al. 1986; Kidwai and Amjad 2001, Fowler et al. 2008). Leis et al. (1986) reported that *Thunnus* spp. and *K. pelamis* larvae were up to 100 times more concentrated within 200 m of a coral reef than in oceanic waters. Previous research by Leis et al. (1993) indicates strong changes in the larvae assemblages in the near reef waters where habit and topography change significantly. We could not identify the *Thunnus* larvae up to the species level. However, we assume that the major share could be *T. albacares* (yellowfin tuna) as it is the most abundant species in this genus distributed in the region. The number of larvae of *K. pelamis* and *Thunnus* spp. were found to be slightly lower compared with other tunas (*E. affinis* and *Auxis* spp.). Sampling for the present study was limited to up to 20 km away from the island, which might be the reason for the lowest abundance of skipjack tuna which usually prefer offshore or deeper waters to spawn (Matsumoto et al. 1984).

The large number of zero values in the data set restricts us from performing ANOVA to check any statistically significant variation in the larvae abundance with respect to sampling distance (Rooker et al. 2013). GAM also failed to predict the abundance of tuna larvae with respect to the sampling distance. However, the present study observed a pattern of

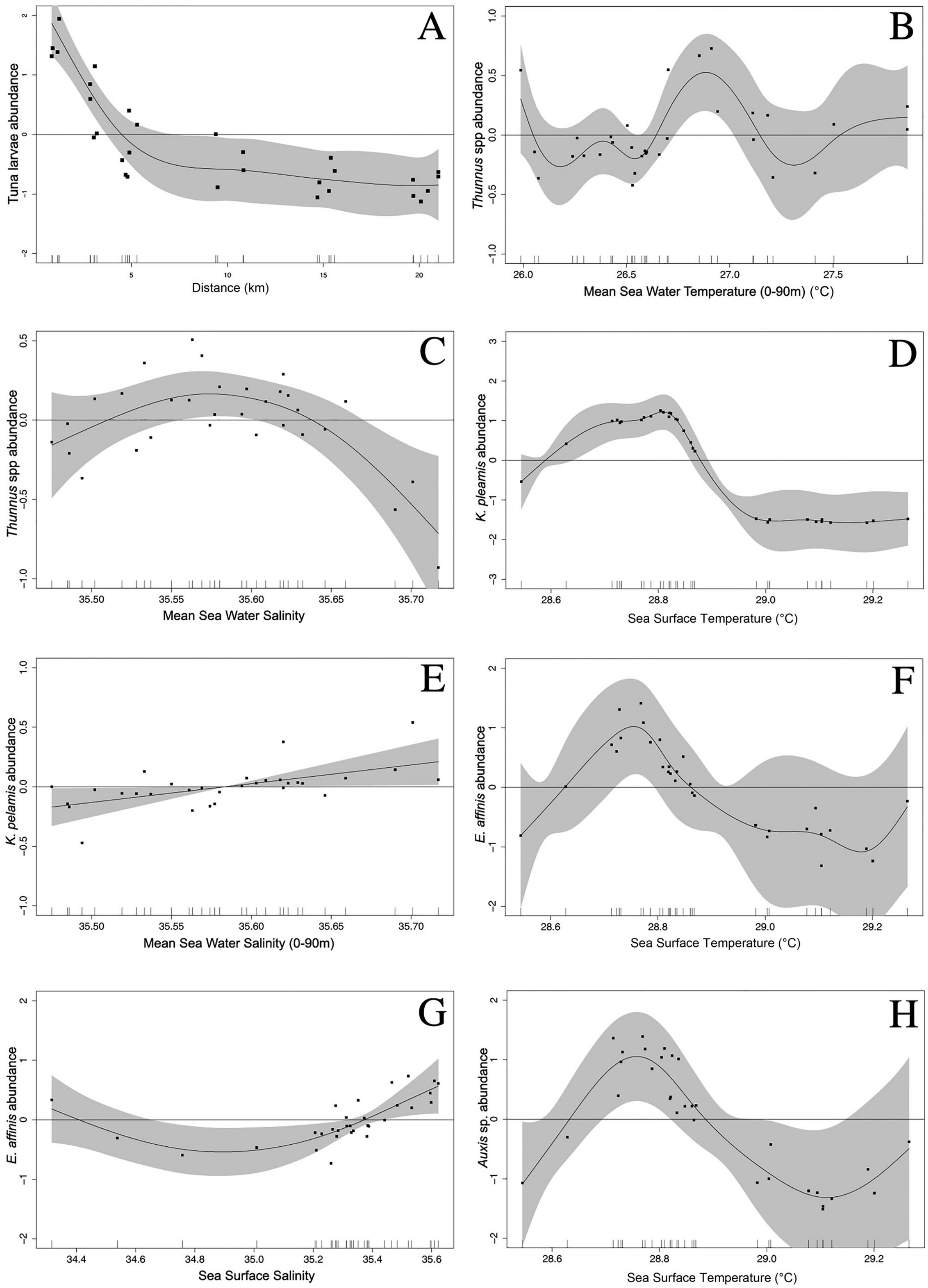

Figure 5. Fitted line (solid) and 95% confidence intervals (shaded area) for the additive effects of significant environmental parameters (sea surface temperature, mean seawater temperature, sea surface salinity, mean seawater salinity) on the presence of various tuna larvae species from the best-fit GAM models. Tick marks on the x-axes represent the location of the data points and the closed circles represent the residuals. The 0 value on the y-axes and the solid line indicate the parametric term of the model (intercept). A, relationship between distance and total tuna larvae abundance; B–H, effect of environmental variables on the abundance of *Thunnus* spp. (B, C), *K. pelamis* (D, E), *E. affinis* (F, G), *Auxis* spp. (H).

Table IV. Results of the generalized additive models with binomial errors for the presence/absence for the larvae of four tuna species for which significant larval abundance- environmental parameter relationships were detected.

Species	Environmental variables	Adjusted R^2	Deviance explained	GCV
T. albacares	Mean sea water temperature (0–90 m), mean sea water salinity (0–90 m)	0.58	78.9	0.12
	Sea surface temperature, mean sea water salinity (0–90 m)	0.37	54.3	0.1253
	Sea surface salinity, mean sea water salinity (0–90 m)	0.308	49.3	0.1363
	Sea surface temperature, mean sea water temperature (0–90 m)	0.198	46.2	0.1723
	Sea surface temperature, sea surface salinity	0.164	37.5	0.1613
K. pelamis	Sea surface temperature, sea surface salinity	0.69	81.3	0.0326
	Sea surface temperature, mean sea water salinity	0.67	80.6	0.0361
	Sea surface temperature, mean sea water temperature (0–90 m)	0.67	80.2	0.035
	Mean sea water temperature (0–90 m), mean sea water salinity (0–90 m)	0.48	69.7	0.0576
	Sea surface salinity, mean sea water salinity (0–90 m)	0.148	35.5	0.0724
E. affinis	Sea surface temperature, sea surface salinity	0.547	75.7	0.1574
	Sea surface temperature, mean sea water salinity (0–90 m)	0.249	54.7	0.2327
	Sea surface temperature, mean sea water salinity (0–90 m)	0.233	53	0.2339
Auxis spp	Sea surface temperature, mean sea surface salinity (0–90 m)	0.436	67.8	0.257
	Sea surface temperature, mean surface temperature (0–90 m)	0.272	52.3	0.2891
	Sea surface temperature, sea surface salinity	0.266	52.2	0.2933

GCV, Generalized Cross Validation Criterion.
Adjusted R^2, deviance explained by the GAM and GCV are presented for each species.

near reef abundance of tuna larvae, except *Thunnus* (Boehlert and Mundy 1994). Koched et al. (2013) indicated a maximum abundance of *Thunnus* larvae in offshore stations, suggesting that spawning usually take place near to the shelf break and the currents push them offshore. All these results are in agreement with the previous findings of variations in the spawning behaviour of these species in world oceans from year-round to seasonal (Matsumoto 1958; Matsumoto 1966). Percentage composition of the larvae of *K. pelamis* is lower in our observations which is in conformity with the previous findings of Boehlert and Mundy (1994). Fowler et al. (2008) reported that *K. pelamis* were most abundant at offshore stations. *Auxis* spp. showed no significant onshore–offshore pattern which is in concurrence with the previous findings of Torres et al. (2011) and Koched et al. (2013).

The present study observed that total tuna larvae abundance is higher on the windward side during SIM compared with SM but was not significantly different. The greatest fish larvae abundance at the windward side was previously reported by Leis et al. (1986) from studies conducted at Lizard Island in the Great Barrier Reef. High *Thunnus* larvae concentrations were observed in the near reef stations on the leeward side of the island even though total tuna larvae are abundant on the windward side. The authors hypothesized that the pattern of currents around the island were the possible reason for this variation. The circulation patterns around coral reefs are very complex, which can have profound influences on the larval distribution of assemblages (Leis 1986, 1993).

High abundance of tuna larvae in the near reef waters indicates that these waters are potential spawning grounds for the oceanic tunas, in concurrence with previous studies (Miller 1979; Leis et al. 1986; Boehlert et al. 1992; Leis 1993; Fowler et al. 2008). The present study records tuna larvae distributed throughout the year, in accordance with the findings of Boehlert and Mundy (1994). Tuna larvae reported from the near reef areas are in early flexion stages, indicating that larvae are possibly spawned in near reef areas and subsequently transported to offshore areas during later stages (Higgins 1970; Leis et al. 1986; Fowler et al. 2008; Koched et al. 2013). As discussed earlier, we were unable to identify 29.3% of the tuna larvae collected, which were mostly in the early-flexion stages, and prefer to stay in the near reef waters. We assume that this gap in the data set is the major hurdle for establishing any statistically significant variation among species.

Variability in spawning preferences among tuna species in the world oceans and the influence of various physiochemical and oceanographic parameters in the spawning pattern and larval distributions of tuna species are confirmed by various studies (Boehlert and Mundy 1994; Reglero et al. 2014; Laiz-Carrión et al. 2015; Dominigues et al. 2016). GAM indicated mean seawater temperature and mean seawater salinity are the major environmental parameters influencing the abundance of *Thunnus* larvae. The larval abundance fluctuated highly with mean seawater temperature (0–90 m) and showed highest abundance at 26.5–27°C (Seckel and Young 1977). Previous studies confirmed that tuna larvae are very sensitive to temperature which has a profound influence on their growth, feeding efficiency and predator avoidance (Margulies 1993; Wexler et al. 2011). Models also indicated that *Thunnus* larvae abundance was high in intermediate salinity values and sharply declines after a mean salinity of 35.65. However, in eastern Mediterranean waters, tuna larvae were mainly collected in oligotrophic and mixed waters as shown by their preference for lower chlorophyll *a* concentration (1.4–2.5 mg m^{-3}) and moderate salinity values (37.35–37.75) (Koched et al. 2013). Alemany et al (2010) observed that tuna larvae avoid highest and lowest salinities. However, Boehlert and Mundy (1994) indicated that scombrid larvae prefer waters with low salinity. All the tuna larvae except *Thunnus* showed a similar pattern of abundance with the SST – it shows maximum abundance at around 28.8°C and declines with higher temperatures (Conand and Richards, 1982). However, higher SST levels are reported to have a positive correlation with the growth of the *Thunnus albacores* larvae as confirmed by Wexler et al. (2004). However, this species failed to show a significant relationship with sea surface temperature and sea surface salinity in the present study.

Sea surface temperature and mean seawater salinity significantly influence the abundance of *K. pelamis* larvae. It was also noted that *K. pelamis* larvae were far less abundant at temperatures below 28.8°C; as observed by Conand and Richards (1982) they showed an inverse relationship with sea surface temperature. Previous studies indicated that *K. pelamis*, as the major tuna species caught from Minicoy Island, is a year-round spawner at the equator and more seasonal at higher latitudes (Raju 1963; Matsumoto 1966; Uchida 1981a, 1981b; Nishikawa et al. 1985), and their larvae are usually found at temperatures above 24–25°C although they have been collected at 22.1°C (Matsumoto et al. 1984). *Katsuwonus pelamis* showed a positive linear relationship with mean seawater salinity (0–90 m) which is contrary to the finding of Conand and Richards (1982) of no influence. The spawning seasons of *K. pelamis* and *T. albacares* near Hawaii begin when sea surface temperatures are rising from the annual minima of 22.5–23.5°C and end when temperatures begin to decline from the maxima of 26.5–25.0°C (Seckel and Young 1977).

The present study indicated that sea surface temperature and sea surface salinity are the major environmental variables responsible for the abundance of *E. affinis* larvae. Spatial variations in the environmental parameters can influence the distribution and abundance of fish larvae as reported by various researchers (Boehlert and Mundy, 1993, 1994). However, previous studies indicated that tuna larvae avoid more eutrophic and saltier waters especially in oceanic islands (Koched et al. 2013). *Auxis* spp. are also diverse in their spawning strategies from year-round to seasonal spawning (Uchida 1981a, 1981b) and are found over a broader temperature range (21.6–30.5°C) than *Thunnus* or *Katsuwonus* (Richards and Simmons 1971). Sebates and Recasens (2001) reported that larvae of *Auxis* species showed high seasonal variability in Mediterranean waters. *Auxis* species also showed an affinity towards lower SST conditions and a high tolerance for temperature variations as observed by various studies in Mediterranean waters (Richards and Simmons 1971; Uchida 1981a, 1981b; Sebates and Recasens 2001; Koched et al. 2013). All the four species of tuna larvae were highly diverse in their preferences for oceanographic parameters (Alemany et al. 2010; Koched et al. 2013). Hence, it is worthwhile to note that better understanding of the prevailing environmental conditions is critical to address larval ecology and to demarcate the potential spawning grounds for different tuna species. All these studies confirm the regional variation in their preferences and tolerances to various environmental parameters.

The present study shows that the environmental parameters are highly variable between stations among transects, indicating the complex nature of the oceanographic characteristics of the islands (Boehlert and Mundy 1993; Torres et al. 2011; Marcedo-Soares et al., 2012). However, mesoscale oceanographic characteristics of the waters have profound influences on the distribution of tuna larvae along with the biological and environmental characteristics (Torres et al. 2011; Rooker et al. 2012; Domingues et al. 2016; Cornic and Rooker 2018). The studies of Bakun (2006) and Torres et al. (2011) indicated high tuna larvae abundance around oceanic islands associated with frontal areas and eddies that could act as convergence and retention zones (Logerwell and Smith 2001; Govoni et al. 2010; Sabates et al. 2013). Later, this was confirmed by Cornic and Rooker (2018) in the abundance of *T. atlanticus* in the Gulf of Mexico. Circulation of water around an island plays a key role in larval assemblages and their dispersal (Alemany et al. 2010). In this study, we have not considered any mesoscale features for the analysis. These conclusions from other parts of the world oceans emphasise the role of mesoscale processes and their dynamics in regulating larval abundance and dispersal patterns, in association with biological dynamics and chemical characteristics.

It is suggested that the high abundances of scombrid larvae near islands may be related to habitat characteristics that promote higher larval survival than in oceanic waters (Nishikawa and Ueyanagi 1991). No research has been carried out on the spatial distribution of tuna larvae around the Lakshadweep Islands. Our study provides initial information on the on–offshore and near reef abundance of tuna larvae from the area, which is highly essential for the conservation of these spawning grounds for the sustainable management and effective utilization of these resources. However, it is suggested that caution has to be exercised when considering the model descriptors for predicting larvae abundance of various tuna species since the study is based on a limited data set. We recommend that further studies with larger data sets are required to assess the pattern of spatial distribution of the larvae and to understand the influence of various environmental parameters on their abundance. Future studies also should address physical oceanographic parameters such as currents and circulation patterns, fronts and gyres, which are very active around oceanic islands, to understand larval ecology and dispersal patterns more accurately.

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