Remotely sensed chlorophyll: a putative trophic link for explaining variability in Indian oil sardine stocks

RUNNING HEAD:
Satellite chlorophyll as a surrogate of sardine biomass

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ABSTRACT
The landing of Indian oil sardine, *Sardinella longiceps* Valenciennes, 1847 along the southwest coast of India is highly variable. A few physical parameters and processes correlated with sardine landing could not establish a flawless connection, and explain the phenomena of inter-annual variability. Earlier researchers indicated that the probable appearance and disappearance of sardine is an active movement in search of food and congenial conditions. But, no specific study has been carried out to explain the variability of sardine catch based on chlorophyll availability on a synoptic scale. An attempt is made in this study to correlate variability in chlorophyll-a with sardine landings along the waters of southwest coast of India. We have estimated monthly averaged surface phytoplankton biomass along the waters of southwest coast of India from the shoreline upto 200 m isobath for ten years from SeaWiFS ocean colour data. This estimation is compared with the biological calendar of Indian oil sardine. The average chlorophyll-a for the bloom initiation month (1998-2006) matches very well with oil sardine landings. The results imply that the concentration of chlorophyll during the bloom initiation month can be used to assess the quantum of fish that recruit into the population. Finer scale spatial variations in the chlorophyll along the coastal waters help in deciphering the migratory pattern of sardine during their active breeding phase. This study shows that 39\% of inter-annual variability in fish landings is related to availability of chlorophyll-a during the bloom initiation month.

ADDITIONAL INDEX WORDS:
*Upwelling, fisheries, ocean colour, phytoplankton, southwest coast of India.*
INTRODUCTION

The inter-annual variability in the landings of Indian oil sardine, *Sardinella longiceps* Valenciennes, 1847 (mentioned hereafter as sardine) has been explained as an outcome of seasonal variability in the marine environment (Hornell, 1910). Based on the physical parameters and processes such as sea surface temperature, rainfall, sea level and upwelling, indices relating to total sardine catch with environmental factors are formulated (Longhurst and Wooster, 1990). These indices, formulated based on a correlation between sardine catch with rainfall, wind stress and sea-level, failed with time due to large variability in landings and correlated factors (Madhupratap, Shetye, and Nair, 1994). Failed correlations should not be dismissed summarily on the assumption that data were faulty, the criteria for comparison were ill-founded, or the relation spurious; rather, the cause and effect should be explored in detail to explain the phenomena (Skud, 1983). There are several inter-related factors which are responsible for the recruitment of fishes and their abundance. The estimation of all environmental variables responsible for this is perhaps a difficult task. Surplus models, recruitment models and similar time series models globally were having limited success. Changes in physical factors affecting marine food web based studies gained more relevance due to this. The concepts of fish stock assessment, rather concentrates now on predicting the expectant biomass based on ambient environment changes which have a trophic link (NRC, 1999; ICES, 2000).

Biological studies suggest an extended spawning period from May to September for sardine (Antony Raja, 1969; Hornell, 1910; Hornell and Nayadu, 1924; Prabhu and Dhulked, 1970). After occlusion from the egg, larval development is rapid in sardine with yolk sac absorption taking place in three days (Nair, 1960). These larvae will undergo their critical first feeding period almost immediately after yolk absorption (Hunter, 1981; Lasker, 1975; Lasker, 1981). The earliest spawned and survived individuals will be recruited to the fishery by the end of the spawning period, which in turn determines the yearly landings. Thus, larval ecology decides the later abundance of recruits to the fishery. Collating various information cited on young, juvenile and adult sardine and their feed during spawning period (Devanesan, 1943; Hornell, 1910; Hornell and Nayadu, 1924; John and Menon, 1942; Van der Lingen, 2002) we could confirm that the larvae is predominantly a surface and column feeder, phytoplankton forming the major group, dominated by diatoms like *Fragillaria oceanica*, *Pleurosigma* sp. and *Coscinodiscus* sp. (Kuthalingam, 1960; Nair, 1959).

Sardines feature fine-meshed filtering apparatus in their gill-rakers (Van der Lingen, 2002), with more than 130 gill-rakers on the lower part of gill arch. They are able to filter smaller particles. Therefore, they thrive from the availability of very tiny particles that may distinguish some of the
coastal waters through which they must migrate even in good conditions, and that may predominate throughout their range of distribution (Bakun and Broad, 2003). Moreover, sardines are serial batch spawners (as are anchovies, sprats, tunas, etc.). They spawn for several days during extended spawning seasons. Thus as sardines employ the combination of their migrating capabilities, their ability to feed on very small particles, and their serial spawning habits, which calls for the importance of studying sardines along with their feed availability during the spawning season.

Hjort-Cushing hypothesis (Cushing, 1974; Cushing 1990; Hjort, 1914) refers to critical first feeding period and the timing of spring phytoplankton bloom. In the case of sardine larvae, the bloom deciding its biology is an upwelling induced bloom, the bloom initiation time and intensity is the only variation that could be accounted for changes in the food supply to sardine larvae. These variations in food supply between different years will be reflected in the larval development and further recruitment of sardine into the fishery. This aspect was not examined in the earlier studies on sardine landing variability.

Sardine performs a normal migration from offshore to coastal waters and vice versa coinciding with the customary wind conditions (Hornell, 1910 b). A gradual increase in temperature within the range of 26 to 28°C is favourable for the inshore migration of the juveniles and with rise of temperature (above 29°C) during March to May they disappear to deeper waters (Chidambaram, 1950). The specific gravity of water, which is above 1.023 during March to May months, also promotes the disappearance of the shoals. The shoreward migration of spawners during monsoon as well as their outward migration to deeper waters during post-monsoon months is for feeding (Nair 1959) on the luxuriant growth of phytoplankton which bloom up during the on-set of monsoon (Chidambaram, 1950; Hornell, 1910b; Hornell and Nayudu, 1924; Nair, 1953). The longitudinal migration either way is an excursion from offshore to inshore waters and vice versa due to availability of food and congenial hydrographical conditions (Devanesan, 1943).

The shoals start disappearing from the northern region first, followed by southern Malabar area. During April to September, the shoals of spawners and juveniles migrate from offshore to inshore all along the west coast following the onset of bloom (Antony Raja, 1972). This observation suggests a northward migration of sardine steadily during southwest monsoon period and retrogression from north to south in the northeast monsoon phase (Figure 1). Lack of continuous seasonal information to characterize synoptic scale variability in chlorophyll concentration of the region was an impediment to verify the food availability between different years to explain the inter-annual variability in sardine landings. Also, it was not feasible to study the spatial and temporal variations in chlorophyll
concentration in these areas due to non-availability of in situ data. With the advent of remote sensing, however, this was possible with ocean-colour data. Platt, Yaco, and Frank (2003), applied remotely sensed ocean-colour data as a direct evidence for a putative trophic link and suggested it as an important link in future analyses of dwindling fish stocks. Time series phytoplankton cycle derived from satellite data can be used to construct a variety of ecological indicators of the pelagic system useful in ecosystem-based management (Trevor Platt et al., 2009).

Remotely sensed sea-surface-temperature (SST) and ocean-colour images revealed eddy and fronts. These features frequently coincide with areas aggregating fish species due to enhanced phytoplankton biomass and primary production which in turn is linked with changes in nutrient supply or mixed-layer depth. As higher plant biomass is associated with zooplankton, one might expect to add supplementary information on fish stock distribution from ocean-colour pigment fields. In an attempt to differentiate the relevance of food over other environmental factors like temperature in fish aggregation, colour patterns offered better information regarding the location of Albacore tuna (Laurs, Fiedler, and Montgomery, 1984). It was originally assumed that tuna prefers to reside within certain limited temperature ranges, thus explaining their aggregation at a temperature front. In instances where colour and SST fronts were spatially separated, they found that tuna actually tend to aggregate on the clear side of a colour front.

Ocean-colour pigments are relevant in detecting a bloom. Fragmented observations in the waters of southwest coast of India hypothesized two seasonal blooms: (i) upwelling blooms, coinciding with the arrival of pre-spawning adults during May-June, and (ii) winter blooms, in September-October coinciding with the main fishery for juveniles (Bensam, 1964). For sardine, a filter feeder, the amount of food ingested depends on chlorophyll concentration as well as copepods present in the ambient waters; better availability of food is expected in chlorophyll rich waters. In the present study, variability in chlorophyll along the waters of southwest coast of India had been quantified from satellite data, and related to annual variability in the sardine landings. The synoptic scale spatial and temporal changes in chlorophyll-a were useful in explaining the appearance and disappearance of sardine shoals along the coastal waters.

**STUDY AREA**

The entire sardine fishing ground off the southwest coast of India, extending from 5°N to 15°N was considered for the study. The seaward limit of the study area extends up to outward edge of the continental shelf (200m isobaths) (Figure 2). Figure 1 explains the schematic representation of
sardine movement, but the actual dwelling area of sardine is segregated in the satellite image by following the depth contour as envisaged in the Figure 2. The spatial extent of the study area was determined in concurrence with earlier observations (Longhurst and Wooster, 1990). The coastal zone current characteristics and environmental setting described in an earlier study (Dinesh Kumar and Srinivas, 2007) also defines this study area as a narrow continental shelf domain with strong upwelling and downwelling signatures.

METHODS AND MATERIALS

Data on marine fish landings in India for the period 1985-2006 published by Central Marine Fisheries Research Institute (Srinath et al., 2006) have been used. 316 samples of sardine were collected from the major sardine landing centre at Cochin for length and weight measurements during the study period. Sardine catch is dominated by 0- group individuals, viz., measuring ≤ 14 cm total length (Pauline Dayaratne and Jakob Gjøsaeter, 1986), spawned during the earlier spawning period starting from May (Table 1). The entire breeding activity of sardine is confined to coastal waters with an active artisanal fishery (ring seines, purse seines and shore seines), which responds with vital fishing efforts depending on fish availability. Fishing along the coastal waters is restricted for mechanized trawlers during a period of 45 days starting from 15 June. The artisanal sardine fishery comprising of motorized and non-motorized country crafts is active during this period also. Decrease in sardine fishery within the study area was not reflected as heavy landings elsewhere, thus ruling out the possibility of migration of sardines from the study area. Hence, it is assumed that the sardine landings within the study area are representative of stock abundance (Longhurst and Wooster, 1990). This assumption holds good since the present study is restricted to a time period, when there was relatively little change in the composition of fishing crafts and gears.

Monthly averaged chlorophyll maps at 9 km spatial resolution derived from Sea-viewing Wide Field of view Sensor (SeaWiFS) data for the period January 1998 - December 2006 was downloaded from the website http://oceancolor.gsfc.nasa.gov/cgi/l3. The optically sensitive constituents such as suspended solids and yellow substance in CASE II waters in this region (Menon et al., 2005; Menon et al., 2006) were tackled during extraction of chlorophyll-a from the composite image using an algorithm for masking turbid waters (Bricaud and Morel, 1987). A trend between sardine landing and chlorophyll-a during the study period was found using the polynomial trend line, which was giving the best fit. Coefficient of determinant was worked out for quantifying the variability in sardine landings and chlorophyll-a during the bloom initiation month.
RESULTS

The variability in sardine landings, chlorophyll variability and chlorophyll during upwelling bloom initiation were examined for explaining the inter-annual sardine variability and sardine migration in the coastal waters.

**Sardine landing variability:** Sardine landing data reveal inter-annual variability since 1925 with an increasing trend during the study period (Figure 3). Sardine landings showed a drastic decline in 1985 and 1994 which alternated with very high landings of Indian mackerel during these two years. Marine fisheries of the southwest coastal waters is characterized by the predominance of pelagic fish resources dominated by sardine and Indian mackerel (*Rastrelliger kanagurta*), which supports the western Indian Ocean’s largest coastal pelagic fishery. Alternating pattern of abundance between these species could have been the reason for these two major falls.

The landing pattern of these two species (Figure 4) along this coast could be compared to the alternating patterns of abundance between sardine and anchovy observed in other upwelling areas of the world. The study period (1998-2006) was a sardine dominant period (period of high sardine and low mackerel). Figure 4 shows a sardine revival phase and the period reflects an ideal phase for the study of sardine without interference from the mackerel fishery.

**Chlorophyll variability in the study area:** Observed chlorophyll in the study area during 1984-2006, ranged from 0 to 6.25 mg/m$^3$ with a mean value of 0.32 mg/m$^3$ and a standard deviation of 0.59 mg/m$^3$, indicating that the chlorophyll available in the coastal waters was highly variable. SeaWiFS chlorophyll values in the study area remains within the maximum-minimum limits of *in situ* chlorophyll (Figure 5) except for the month of August 2002 (6.557 mg/m$^3$) which may be due to an unusually high upwelling bloom.

The chlorophyll-a concentration remained high during May to October, but the peaks varied from year to year. Period of higher chlorophyll-a concentration matches with the active breeding period of sardine (Figure 6). The biological calendar of sardine (Figure 6) commences with the entry of spawners in May, followed by fresh juveniles during July-August. During September to December, the adults occur in reduced numbers, whereas the significance is taken away by the access to large shoals of juveniles. They, however, get numerically reduced in January-February and, subsequently disappear, and then appear during May-July. With the onset of pre-monsoon showers or southwest monsoon rains, they move towards the inshore waters with the gonads in various stages of ripening. The spent and resting adults, on the other hand, appear in small quantity along with their juveniles.
during January-February, and disappear in the following months along with the juveniles but re-enter for their second spawning along with the virgin spawners. For numerically representing the average chlorophyll which determines the active breeding phase, chlorophyll concentration ≥1 mg/m³ can be a threshold mark as calculated for the entire study period (Table 2). The average monthly chlorophyll-a values in May reach a threshold level of above 1 mg/m³ (Table 2). We have examined the suggestion (Madhupratap et al., 1994) that a mismatch viz. an early spawning and a time lag in development of food (through a break in monsoon or upwelling) would be detrimental to recruitment.

**Sardine landings vis-à-vis chlorophyll during bloom initiation:** We tested the null hypothesis that the variability in sardine landings was independent of fluctuations in average chlorophyll concentration during bloom initiation month. We could confirm that 39% variability in sardine landings was related to average chlorophyll-a concentration during the bloom initiation month. Figure 7 clearly depicts an increase in chlorophyll-a, which is associated with high landings (match) and decrease with reduced landings (mismatch) except for the year 2002. Since, chlorophyll availability cannot be the only factor affecting the sardine biomass, there are other factors also affecting sardine biomass. But, the availability of chlorophyll rich water in the bloom initiation month will result in better survival of sardine larvae. Early food availability provided by an upwelling bloom, indicated as higher chlorophyll-a in the chart, is reflected in increased sardine landings as many of the total larvae recruited were able to survive because of surplus food. Even though SeaWiFS data is short, the data do indicate a definite link between chlorophyll-a and sardine landings. Early initiation of phytoplankton bloom may not be sufficient to ensure a higher survival of sardine larvae in the same year, but definitely a necessary condition as envisaged in the study. This was reflected in the sardine landings as the fishery was dominated by 0-year class fishes (Table 1). An unprecedented blooming was observed in 2002 when chlorophyll-a values were the highest during the study period. Thus, the year 2002 was exceptional to have a low-chlorophyll in May followed by an unanticipated high chlorophyll period (Figure 6). Since the spawning period of sardine is protracted, high survival of later spawned larvae in the years when bloom development delayed could make up for poor survival of early spawned larvae.

Gut analysis shows that sardine being a filter feeder, sardine ingests the particulate phyto and zooplankton available in its ambient waters. The phytoplankton bloom (mostly diatoms and dinoflagellates) results in better productivity enhancing the micro zooplankton and zooplankton in the Arabian Sea (Madhupratap et al., 2001). This is evident in this study as zooplankton biomass
observations in the study area also show several peak values during the months (September-December) following increased chlorophyll-a (Figure 8).

**Seasonal appearance of sardine and chlorophyll:** The present study clearly reveals the synoptic scale temporal changes (1998-2006) with respect to chlorophyll availability in the three prominent sardine landing maritime states (Figure 9) of India – Kerala, Karnataka and Goa. Figure 9 illustrates how chlorophyll rich waters appear earlier in the south (Kerala coastal waters) and move gradually northwards, and the pattern reverses during the retrieval of monsoon. The changing intensities of chlorophyll in the coastal waters (area under the graph for each year in Figure 9) of the states describe the possible appearance and disappearance of sardine shoals during the active breeding phase.

The variation in quarterly sardine landing in each maritime state (Figure 10) is proportional to the changing intensities of chlorophyll in the respective coastal waters. This shows an aggregation response of sardine larvae to chlorophyll concentrations.

**DISCUSSION**

There was very little change in the fishing effort during the study period with 2,38,772 fishing crafts in 2005 (CMFRI, 2005) in comparison to 2,39,000 crafts in 1997 (Sathiadhas, 2006). Thus, the increase in sardine landings during the study period despite steady fishing effort indicates a direct trophic link as reason for the revival of the fishery. Sardines possess fine branchial apparatus; feed predominantly by filter feeding on phytoplankton and zooplankton in ambient waters. Chlorophyll-a in a given area, as an index of phytoplankton biomass, is capable of assessing the food availability for sardines.

Summer chlorophyll-a concentration estimates from the study area is reported to be 0.1 to 5 mg/m³ for a normal distribution and can be very high from 5 to 10 mg/m³ during bloom period (Raghavan et al., 2006). Heavy blooms of *Fragillaria oceanica* were observed in 1949 and 1953 during the rebuilding of sardine stock after the population crash of 1940’s (Nair, 1953; Nair and Subramanyan, 1955), suggesting and strengthening the view that advantage of an early bloom will result in the survival of more larvae which otherwise would have perished due to lack of food.

Life cycle of sardine depicted a clear picture of active breeding season from May to September. This coincides with the high chlorophyll concentration seen during May to October every year. Thus, there is a seamless connection of life history and biology of sardine to phytoplankton bloom.
dynamics. This supports the finding that the fish itself times its appearance to exploit the productive southwest monsoon period (Madhupratap et al., 1994). The upwelling bloom can be characterized with respect to its peak amplitude, timing of peak, timing of initiation and duration. In the present study, magnitude of the bloom at initiation is considered for characterization of bloom, which naturally falls in the month of May every year. May is the most critical month showing bloom initiation and starting of active breeding phase of sardine.

A delay in the initiation of bloom in the area results in hampering the congenial conditions for survival of sardine larvae. In the prevailing rough conditions when fishing activity is slackened, there may be an apparent paucity of sardine. But, as we find in the published reports (Antony Raja, 1969; Longhurst and Wooster, 1990) when there was fishing during July-August, it was noticed that the spawners entered the coastal waters due to increase in food production, and migrated beyond the usual fishing belt (30 m depth), for spawning. The spawners again made a re-entry to compete with the juveniles for feeding during September to December. The juveniles entered the coastal waters gradually for feeding during January- March period and steadily migrated to deeper waters with reducing food. Their disappearance initiates first from the northern limits of sardine fishing ground and ends up in the southern areas later.

Recent works on the survival of early life history of fishes elucidates various factors including predation, drift pathways and changing environmental conditions in addition to variation in food (Bakun and Broad, 2003; Cury et al., 2000; Houde, 1987; Legget and Deblois, 1994; Miller et al., 1988). Upwelling in the waters of southwest coast of India is restricted to 5 to 15°N and the variability in physical parameters is manifested in the chlorophyll intensity (Smitha et al., 2008). A correlation between available environmental datasets (SST, sea bottom temperature, surface salinity, surface dissolved oxygen, bottom dissolved oxygen, pH, nutrients, chlorophyll, zooplankton, rainfall, multivariate El Nino Southern Oscillation index, coastal upwelling index and derived SST) and sardine catch from the study area vividly segregate the significance of chlorophyll from other environmental factors in explaining the sardine catch from Malabar upwelling area (Krishnakumar and Bhat, 2008). A similar analysis of data sets is redundant in the context of this investigation. Hence, this investigation focused on food alone, the lone implicated factor chlorophyll-a (as an index of phytoplankton biomass), and explored various avenues of this factor in explaining sardine variability.

A finer scale spatial and temporal pattern of egg and larval stages of sardine in relation to chlorophyll concentration could have yielded a proper model describing the presence or absence of
sardine in coastal waters with a definite chlorophyll range. There are sparse reports of sardine eggs from Quilandy (Devanesan, 1943) and Kozhikode (Nair, 1953) and also descriptions of the larval and post larval stages of sardine in these regions (Nair, 1959). But lack of information on distribution of eggs and larvae emphasize the need for sampling of early life history stages of sardines over many years for determining the annual condition of larval and juvenile sardine in relation to chlorophyll concentrations.

CONCLUSIONS

Variation in sardine abundance could be attributed to variability in physical forcing like upwelling, sea level, temperature, wind stress, rainfall and monsoon conditions (Krishnakumar and Bhat, 2008; Longhurst and Wooster, 1990). However, such an indicator was not a direct trophic link to sardine. The important factors responsible for the offshore-inshore migration appear to be the strength, duration of upwelling bloom and changes it brings about in physico-chemical and biological conditions in the coastal waters. But, a lag phase between upwelling and intense production is notable in earlier studies in this region (Vimal Kumar et al., 2008). Hence, Chlorophyll concentration in coastal waters is the major factor for establishing a trophic link which summaries the above physical and chemical process. An early spawning and a time lag in development of food (through a break in monsoon or upwelling) would be detrimental to sardine recruitment. Consequently, chlorophyll concentration during the bloom initiation month substantially explains the inter-annual variability in sardine landings. The spatial and temporal variations in the intensity of chlorophyll in the coastal waters were reflected in the sardine abundance.

Application of remotely sensed chlorophyll provided a putative trophic link for explaining variation in sardine catches along the waters of southwest coast of India. Remote sensing from satellite offer some solution for the requirement of an entire range of information needed to assess “changing ocean”. But, this information has to be coupled with other appropriate biological data for forecasting fish distribution. Thus, satellite chlorophyll in its present state alone cannot be an alternative to in situ chlorophyll. The absolute chlorophyll present in CASE II waters often get challenged by the turbidity contributed by other optical constituents. It is the judicious application of both satellite and observed data which will help in deducing the correct picture. There are many recent developments in building of trophic models of aquatic ecosystems (Hall and Mainprize, 2004). There is potential for satellite phytoplankton data to serve in future as a surrogate for sardine biomass. Usually, investigations in fisheries biology lack time series environmental or other biological datasets (Longhurst and Wooster, 1990; Madhupratap et al., 1994). The combination of satellite datasets with
fisheries data can lead to robust conclusions. Longer time series will be required to confirm and
determine the large-scale fluctuation in abundance, population crashes and subsequent revival of this
major pelagic fishery in the south west coast of India.

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Table 1. Average length and weight measurements of 316 random sardine samples from a major landing centre.

<table>
<thead>
<tr>
<th>Total Length (cm)</th>
<th>Fork Length (cm)</th>
<th>Std Length (cm)</th>
<th>Gill Girth (cm)</th>
<th>Max Girth (cm)</th>
<th>Mouth Diameter(H) (cm)</th>
<th>Weight (gm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11.64±2.57</td>
<td>10.24±2.28</td>
<td>9.64±2.15</td>
<td>1.77±0.49</td>
<td>1.90±0.52</td>
<td>0.88±0.39</td>
<td>12.58±10.96</td>
</tr>
</tbody>
</table>

Table 2. Estimation of monthly average chlorophyll during the study period indicating a higher value above the threshold during the active breeding season.

<table>
<thead>
<tr>
<th>Month</th>
<th>Average chlorophyll (mg/m³) during 1998-2006</th>
<th>Life stage of sardine</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>0.618333</td>
<td>immature, spent resting</td>
</tr>
<tr>
<td>February</td>
<td>0.540444</td>
<td>immature, spent resting</td>
</tr>
<tr>
<td>March</td>
<td>0.546444</td>
<td>immature, spent resting</td>
</tr>
<tr>
<td>April</td>
<td>0.593778</td>
<td>immature, spent resting</td>
</tr>
<tr>
<td>May</td>
<td>1.158222</td>
<td>maturing, developing virgins</td>
</tr>
<tr>
<td>June</td>
<td>1.858333</td>
<td>maturing</td>
</tr>
<tr>
<td>July</td>
<td>3.957667</td>
<td>maturing, mature, running, partially spent</td>
</tr>
<tr>
<td>August</td>
<td>4.011889</td>
<td>maturing, mature, running, partially spent, spent</td>
</tr>
<tr>
<td>September</td>
<td>3.187778</td>
<td>mature, running, partially spent, spent</td>
</tr>
<tr>
<td>October</td>
<td>1.666556</td>
<td>Immature, running, spent</td>
</tr>
<tr>
<td>November</td>
<td>0.937333</td>
<td>immature, spent resting, spent</td>
</tr>
<tr>
<td>December</td>
<td>0.708</td>
<td>immature, spent resting</td>
</tr>
</tbody>
</table>
Figure 1. Schematic representation of progression of sardine shoals from Vizhingam to Vangurla (Chidambaram, 1950; Hornell, 1910) and their departure in the reverse direction (Panikkar, 1952).
Figure 2. Study area and 3 major sardine landing maritime states displayed in the satellite image from SeaWiFS.
Figure 3. Inter annual variability in sardine landing since 1925.

Figure 4. Comparison between sardine and mackerel landings (1985-2006).
Figure 5. Observed chlorophyll during 1984-2006 for a comparison with monthly SeaWiFS chlorophyll values retrieved for the study area (data source: Indian Oceanographic Data Centre, NIO, Goa).
Figure 6. Monthly satellite chlorophyll concentration for the period 1998-2006 in relation to biological calendar of sardine. Grey coloured columns in the table show the active breeding phase and remaining columns show the passive resting phase.
Figure 7. Comparison between chlorophyll-a concentration during bloom initiation month and sardine landing.
Figure 8. Monthly observed zooplankton biomass during 1984-1996 (data source: Indian Oceanographic Data Centre, NIO, Goa).
Figure 9. Progression of remotely sensed chlorophyll in the three maritime states during the active breeding season of sardine.
Figure 10. Quarterly sardine landing/km of coastline in the three maritime states.