is, thus, simultaneous with or occurs immediately before anthesis (Figure 1 *c*–*f*). (ii) In some flowers opening initiates by the expansion of the apices of the tepals, the stimulus of which then spreads laterally (Figure 1 *a* and *b*). However, what is interesting to note is that the anthers are still in an undehisced state. It takes more than 24 h for these anthers to dehisce.

About 20% of plants in a population show the dual mode of anther dehiscence. The frequency of such flowers per plant varies between 20% and 30%. It takes about 4–6 days for the male flowers to empty their contents.

It is quite possible that the two distinct patterns of anthesis are adapted to two modes of pollination; the lateral opening probably catering to the needs of wind pollination and apical opening for biotic/insect pollination. Even though flowers are inconspicuous and unattractive, a number of diverse visitors like ants, bees, houseflies and sparrows frequent the flowers for different purposes. Bees visit in the morning up to noon; duration of each visit is brief, lasting 6 sec. Ants feed on pollen and houseflies are just casual visitors. Sparrows probably prey on the aphids found in the inflorescences. Therefore, the actual role of insects in pollen transfer remains to be determined.

It is equally likely that the buds with apical anthesis are not able to empty their pollen compared to the ones with lateral opening. This is largely on account of mechanical reasons. There is a considerable space constraint inherent in the floral architecture itself. Presence of bract on one side and floral axis on other apparently keeps the flowers snuggled/squeezed. Anthers after dehiscence unload their contents inside the tepal cavity. Since the tepal opens from the top, only strong wind can take out the pollen. However, those which open laterally have two slits, one on each side. A mild breeze is enough to allow the pollen of such flowers to be carried away.

Male flowers usually differentiate on young shoots which are exserted and tend to be away from the plant body proper (Figure 1 *l*). This is an adaptation to ensure effective pollen dispersal even in small wind currents. Continuous motion of extruded young shoots on slight disturbance or slow wind facilitates pollen dispersal. Had they been amidst the older shoots, dispersal to neighbouring female plants probably would have been hampered.

Female flowers also vary in their behaviour vis-à-vis exposing their stigmas. (a) In nearly 30–40% of flowers in a population, female flowers have a persistent perianth. From this tightly closed perianth the stigma grows and protrudes out at the time of anthesis (Figure 1 *j* and *k*). (b) In many flowers, the perianth withers at an early stage of development leaving behind a naked flower bud and the emergence of stigma marks the beginning of anthesis (Figure 1 *i*).

Under such circumstances, it becomes difficult to ascertain the exact stage of anthesis. However, stigma becomes receptive 24 h after extrusion or opening and is at its peak 72–96 h after anthesis.

Female flowers protected by the perianth are at advantage because at the time of anthesis (14–27 April), the climate of Ladakh is harsh and stigmas are susceptible to desiccation. On the other hand, in flowers where the protruding stigmas are protected by the bracts, the bracts bend at the receptive stage (Figure 1 *j* and *k*) when the stigma attains a length of approximately 2 mm in 3–4 days (Figure 1 *h*).

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Puffer fish menace in Kerala: a case of decline in predatory control in the southeastern Arabian Sea

Since 2006, fishermen in Kerala have been complaining about the extraordinary abundance of puffer fishes (Figure 1 *a*) in the Arabian Sea during the post-monsoon period and the extensive damage it causes to their nets and catch[1,2]. These fishes are able to cut through the nylon nets once they are caught causing extensive damage to the nets (Figure 1 *b*). Also, once within the nets they bite at random on other catch, particularly valuable squids and cuttlefishes (Figure 1 *c* and *d*), decreasing their commercial value. Damage to the nets and catch has not been formally estimated, but is apparently running into several crores of rupees as per newspaper reports. The puffer fishes belonging to family Tetraodontidae are uniquely characterized by sharp, plate-like teeth (numbering four, and hence the family name; Figure 1 *e*) and a spiny or prickly, loose-skinned, rib-less body which can take in water to become a prickly or spiny ball. These

Figure 1. ***a***, A catch of *Lagacephalus inermis* from a trawling vessel at Cochin Fisheries Harbour. ***b***, A trawl fisherman displaying damaged trawl net which is repaired with lighter twine. Squid (***c***) and cuttlefish (***d***) from trawl catch damaged by bites of *L. inermis*. ***e***, Lips of *L. inermis* pulled back to expose the four plate-like teeth.

odd-looking fishes are virtually a no-no as prey for most predatory fishes in the sea because of these characteristics. Besides, parts of their body, particularly the liver and gonads, are also toxic to humans due to the presence of tetradotoxin (TTX), which is a neurotoxin causing asphyxiation and death.

In order to study this sudden increase in puffer fish biomass in the Arabian Sea off Kerala, we assembled the catch (landing) statistics of all species of puffer fishes occurring in Kerala from the National Marine Living Resources Data Centre (NMLRDC) at the Central Marine Fisheries Research Institute (CMFRI), Kochi for the period 1970–2011 (41 years). Since we did not have real-time trawl survey data, we assumed that catch from all gears is a fair reflection of biomass in the sea. We then sifted through the literature on stomach content data of major predators in the Arabian Sea ecosystem to find out the major predators of puffer fishes. Once the major predators on puffer fishes were identified, we looked at their abundance (catches) during the same time-period in order to discern patterns and trends using correlation coefficients. Random examination of few puffer fish (*Lagocephalus inermis*) stomachs was carried out to identify its major prey as there was no location-specific diet literature. The catch trends of the two major prey groups (anchovies and squids) were then plotted to identify cascading trends.

Tetradontids are demersal mid-level carnivores (trophic level: 3.89)[3] mainly caught in trawls (78%) and also in seines, gillnet and hook and lines. Their catches have been meagre in Kerala during the 1970s, 80s and 90s. From 2006, there has been a steep increase in the catches, and in 2011, within 5 years, it is close to 2000 tonnes (Figure 2). Among the puffer fishes caught, the smooth-backed blow fish, *L. inermis* is the major species (52%) followed by the fat puffers, *Arothron* sp. (45%) and the porcupine fish, *Diodon* sp. (~ 2%; inset, Figure 2). The main season for puffer fish fishery is post-monsoon (October–January; 49%), followed by pre-monsoon (February–May; 36%) and monsoon (June–September; 15%).

The literature on stomach contents of the major predators showed that there are few predators of puffer fishes in the Arabian Sea ecosystem. A major predator identified was the cobia or kingfish, *Rachycentron canadum* (Table 1)[4–7]. This large predatory fish, which can grow up to 2 m and weigh nearly 30 kg is considered a high-priced delicacy, and therefore is a major target of the gillnet fishing fleet. The diet breadth of this species is very wide and the fact that between 8% and 36% of its diet is composed of puffer fishes is significant and indicates its preference for puffers as prey[6,7].

Another major predator of puffer fishes in the ecosystem are the different species of catfishes belonging to the genus *Arius*. These large, long-lived fishes grow to nearly a metre in length and weigh about 5 kg. The puffer fish content in catfish diet is less than 2% (Table 1). Both the catfishes and the cobias have dorsoventrally flattened head and mouth, and consequently their mouth gape is extraordinarily wide. This would enable them to gulp a bloated puffer fish with ease, although their teeth are not very sharp or strong.

Two fast-swimming, large, pelagic predators in the ecosystem also have puffer fishes as their prey (Table 1), namely the skipjack tuna (*Katsuwonus pelamis*) and the Kingseer (*Scomberomorous commerson*). Although the percentage of puffers in the diet of skipjack tuna is high (~ 10), these fishes are inhabitants of the oceanic realm, particularly the Lakshadweep Islands, and therefore, are not expected to play a significant trophic role in the coastal ecosystem. The percentage of tetradontids in kingseer diets is very small and it forms only a small fraction of the more than 25 diet components[5]. Other likely predators of puffer fishes are the sharks, for which we could not gather diet literature from Indian marine ecosystems. Carcharhinid diets from other marine ecosystems of

Table 1. Predators of tetradontids in Indian marine ecosystems

Predator	Scientific name	Average % in diet	Main season	Trophic level	Location	Reference
Skipjack tuna	*Katsuwonus pelamis*	~ 10*	September–October	3.80	SW coast	4
Kingseer	*Scomberomorous commerson*	< 1	July–September	4.30	SE coast	5
Catfish	*Arius serratus*	< 2	Unspecified	4.15	SW coast	6
Cobia	*Rachycentron canadum*	~ 8	Unspecified	4.32	SW coast	6
Cobia	*Rachycentron canadum*	~ 36	February, May–June	4.39	NW coast	7

*Coral reef-associated puffer fishes.

the world indicate they are heavy predators on puffer fishes; for instance, nearly 10% of the diet in tiger sharks from Western Australia[8].

Our analysis of the estimated catch of the puffer fish predators indicates interesting trends, particularly of the main predators, cobia and catfish (Figure 3). The catfish shows a drastic decline in its catches, and from 1985, it has the status of a collapsed stock[9]. Although the consumption rate of catfishes on puffer fishes is relatively small, the catfish biomass in the ecosystem was relatively large (more than 30,000 tonnes fished biomass) during the 1970s and 80s. On the other hand, the cobia which has a relatively small biomass has come under severe fishing pressure lately, and its catches have declined by 44% from 2007. Sharks which are the major predators in any marine ecosystem (although we have no direct evidence of their consuming puffer fishes in the Arabian Sea), have declined by more than 70%, and they have been classified as close to depletion[9]. The Pearson correlation coefficients of puffer fish catch with catfish (–0.236) and sharks (–0.219) were negative, but the relationships were not significant ($P > 0.05$), because of the inherent variability in long-term (41 years) catch trends. The catfish depletion has probably played only a minor role in puffer fish catch increase as it has happened much earlier (1980s). On the other hand, the start of decline in cobia catch in 2007 and the start of increase in puffer catch in the same year are strongly coincidental. Overall, the Pearson correlation coefficient for puffer fish and cobia catch was positive and significant (0.363, $P < 0.05$, 41 years), but when compared from 2007, the relationship was strongly negative and very weakly significant (–0.761, $P = 0.135$, 5 years). The high percentage of puffer fishes in the diet of cobias supports the inference that it is the sudden decrease in cobia biomass that has played a major role in the increase in puffer fish catches after 2007.

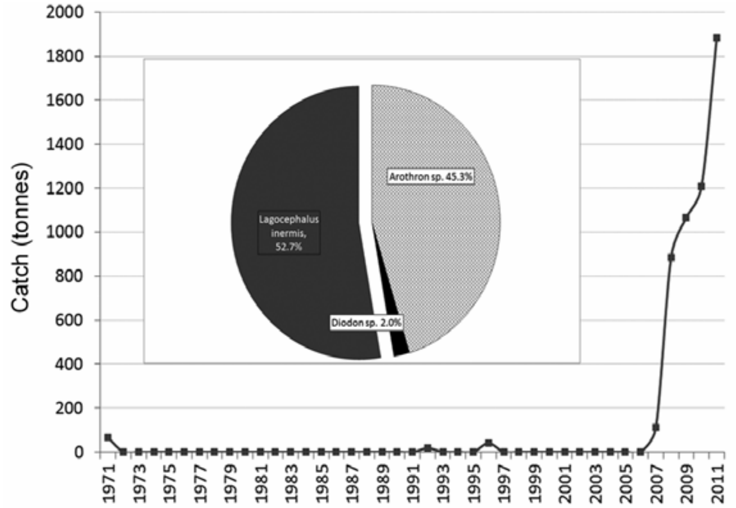

Figure 2. Catch trend of puffer fish in Kerala with steep increase after 2006. (Inset) Percentage of species composition of puffer fish.

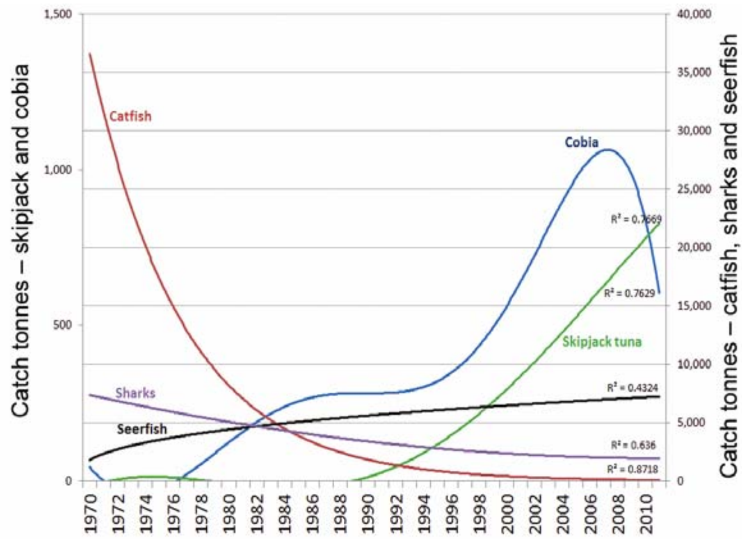

Figure 3. Regression trends of estimated catch for the major predators of puffer fish. Regression coefficients are shown at the end of each line.

The two other predators of puffer fishes show increasing trends in catches (Figure 3). The seerfishes which are a group of large pelagic fishes with high market demand show much fluctuation in catches, but have an overall rising trend. The skipjack tuna which is an oceanic species, with the main biomass concentrated around the Lakshadweep Islands shows a steep increase in catch from

1990, mainly because of expansion of fishing grounds by mainland boats to Lakshadweep waters. Moreover, the puffer fishes in the diet of skipjack tunas are mainly coral-reef associated species[4] (*Canthigaster* sp. and *Tetradon* sp.). Quite clearly, both these predators have a large presence in the current Arabian Sea ecosystem, but because of their feeding strategy, are not likely to have exercised any control over puffer fish biomass in the coastal ecosystem.

The above data lead us to believe that there are signs of the beginning of a trophic cascade in the Arabian Sea resulting in increased biomass of puffer fishes from 2007. Certainly, there are signals of a predation-induced top-down effect on one mid-level carnivore population in the Arabian Sea off Kerala. The *Encyclopedia Britannica* defines a trophic cascade as an ecological phenomenon triggered by the addition or removal of top predators and involving reciprocal changes in the relative populations of predator and prey through a food chain, which often results in dramatic changes in ecosystem structure. Until the work on trophic cascades in a formerly cod-dominated ecosystem in the northwest Atlantic, it was believed that the trophic cascades of the kind observed in land or in lakes after removal of top predators do not often occur in the open sea[10]. This seminal work[11] showed that as the cod populations collapsed on the eastern Nova Scotia shelf, the biomass of small pelagic fish increased by 375% and the benthic invertebrates (shrimp, snow crab), once prey of demersal fish, also increased strongly. Subsequently, there are other reports of similar species shifts from other seas in the temperate regions of the world, while similar evidences from open tropical seas are limited[12].

The puffer fish abundance of recent times in India is not restricted to Kerala; it has also occurred in the neighbouring states of Karnataka[13] and Tamilnadu[14]. The phenomenon of fishing down the food web (excessive removal of top predators in the ecosystem) has been reported along the Indian coasts, particularly the southeast coast[15,16]. And therefore, we presume that a similar loss of top-down control of predators may be in operation in these ecosystems as well.

In the Arabian Sea, the loss of predatory control on the puffer fish biomass due to depletion of its main predators (mainly cobia) is probably the principal cause for the increase in the biomass of its immediate prey. When we looked for cascading effects on the prey of puffer fishes (anchovies and squids), we did not get a clear trend. It is possible that in tropical seas, the high biodiversity, large diet breadth of many predators and the relatively fast generation times of many species prevent the occurrence of clear trophic cascades. It has been stated that trophic cascades are most common and clearly evident in low-diversity benthic marine ecosystems[17]. Besides the increase in puffer fish abundance is fairly recent (within the last 6 years), and this time is probably not sufficient enough for ecological-scale population changes to occur. A close watch and monitoring of population biomass changes and abiotic factors is necessary to discern trophic cascades in tropical seas such as the Arabian Sea. Presently, fishermen have found value for this unwanted catch by salting and drying the fish for exports[2,14].

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