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# Puffer proliferation in tropical coastal waters: influence of indiscriminate trawling

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Intensive mechanized fishing has induced marked alterations in coastal marine ecosystems resulting in proliferation of low-value, nuisance species in marine fish catches. Assessment of 75 shrimp trawl catches taken in the near-shore waters off Goa, west coast of India during active fishing periods from 2006 - 2008 revealed that the demersal pufferfish, *Lagocephalus spadiceus* constituted  $\approx 27$  % by weight of the trawl catch during January – March, and its catch was inversely related to prey and predator species. Sub-tidal rock reefs and submerged rocky patches in the study area offer suitable substrates for spawning, and the predominance of adults during these months suggesting spawning migration. Comparison of the present data with published literature indicates a significant reduction in puffer predators (catfishes). Excessive removal of high-value predators favours the proliferation of pufferfish and its establishment as a meso-predator, probably triggering a potential trophic cascade. The paper discusses the role of removal of High Trophic Level (HTL) species in the proliferation of a meso-predator and its impact on ecosystem function.

[Keywords: Meso-predator, Predator removal, Proliferation, Pufferfish, Trawl catch]

#### Introduction

Coastal marine ecosystems are becoming increasingly vulnerable to elevated levels of anthropogenic activities potentially detrimental to their sustenance and undermine ecological functioning. Large-scale alterations in land-use pattern in the adjoining coastal regions and the use of destructive fishing techniques have resulted in the deterioration of vital marine habitats, pollution, nutrient loading, and removal of top predators and proliferation of nuisance aquatic species<sup>1,2</sup>. The estuarine and near-shore coastal waters of Goa, the west coast of India represent a marine biome afflicted with varied anthropogenic activities<sup>3-5</sup>. Intensive fishing activities for demersal resources have reportedly resulted in the overexploitation of penaeid prawns<sup>6</sup> and various bycatch species'. In light of this, intensive sampling surveys were carried on-board shrimp trawlers to assess the species composition of trawl catches. The present paper reveals proliferation of the pufferfish Lagocephalus spadiceus (Richardson, 1845) in nearshore waters off Goa, west coast of India and discusses the probable causes and potential implications of their proliferation for coastal ecosystems.

## **Materials and Methods**

Goa with a 105 km coastline flanking the Arabian Sea comprises diverse marine habitats including near-

shore sub-tidal soft bottom, submerged rock patches, coral reef patches<sup>8</sup> and mangrove-lined estuaries<sup>9</sup>. Artificial structures including shipwrecks off the coast provide habitat for various demersal fauna<sup>10</sup>. The present observations were undertaken in the 20 m depth region off Calangute (Fig. 1) to enable comparison with earlier published data<sup>11</sup>.

Five trawl hauls (1 - 2 h duration each) were taken once a month on-board 9 m long, single-day commercial trawler. A total of 75 hauls were taken during February – April 2006, December 2006 – May 2007, November 2007 and January – May 2008 with a total effort of 137 hours. Trawl nets with mouth end and cod end mesh sizes of 15 and 9 mm, respectively, were towed at approximately 2 knots (4 km h<sup>-1</sup>) speed. The catch was segregated into pre-determined faunal groups following Prabhu & Dhawan<sup>11</sup>, and each group was weighed for further analysis.

At the shore laboratory, fish samples were identified using morphological, meristic and morphometric methods following Fishbase<sup>12</sup> and other taxonomic literature<sup>13-16</sup>. Life stage determination (adult or juvenile) of fish samples was aided by Fishbase<sup>12</sup>.

Faunal weight is a reliable variable/ parameter for quantitative assessment of trawl catch. For analysing the catch, weight of each epifaunal species/ taxon was standardized to per hour (60 min) haul due to

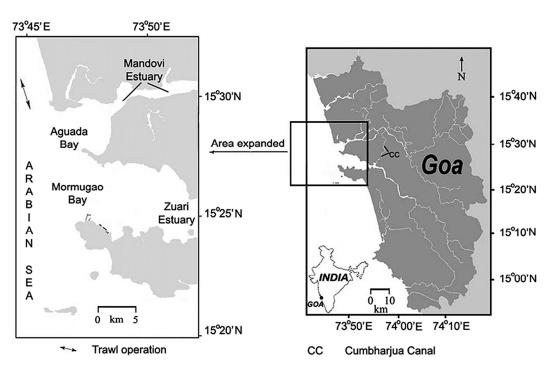


Fig. 1 — Map illustrating trawl operations in the near shore waters of Goa west coast of India

variability in the trawling duration. Monthly averages of fish weights were derived and used for further analysis. Availability of catch data during February, March and April months for three consecutive years (2006 – 2008) facilitated comparisons among the sampling years.

Species-wise marine fish landing data (sharks, catfishes and other carangids) provided by the Central Marine Fisheries Research Institute (CMFRI) for Goa was available only for the years  $1982 - 2004^{(refs. 17-19)}$ . However, CMFRI marine fish landing data for the years 2005 - 2012 is categorized as "Pelagic", "Demersal", "Crustaceans" and "Molluscs", and therefore, does not provide data as specified for earlier years. Hence, the data for catfishes and sharks for the years 2000 - 2012 was obtained from the Directorate of Fisheries, Government of Goa<sup>20</sup>. However, the data for carangids is included in the "miscellaneous species" group, and therefore not available for comparison.

Information pertaining to the trophic level of fishery groups was obtained from Bhathal & Pauly<sup>21</sup>.

# Results

## Total trawl catches

The highest mean catch rates of  $249\pm167$  kg h<sup>-1</sup> were recorded during March 2008 and the lowest of  $40\pm21$  kg h<sup>-1</sup> during April – May, 2007 (Fig. 2). Yearwise comparisons revealed a lack of consistency in

the seasonal patterns across the years. The combined catch rates for the peak trawling season were highest during February – April, 2008 followed by February – April, 2006 and February – April, 2007 (Fig. 2).

#### Prawn catches

The target organisms of the single-day commercial shrimp trawl fishery mainly comprised of five penaeid prawns namely Metapenaeus dobsoni (Miers, 1878), M. affinis (H. Milne Edwards, 1837 [in Milne Edwards, 1834–1840]), Parapenaeopsis stylifera (H. Milne Edwards, 1837 [in H. Milne Edwards, 1834-1840]), Penaeus monodon Fabricius, 1798 and P. indicus H. Milne Edwards, 1837. Analysis of monthwise catch composition of trawl hauls revealed that prawns contributed 8 - 56 % to the total catches (Fig. 3). The highest mean prawn catch rates of 126±34 kg h<sup>-1</sup> were recorded during March, 2006 and the lowest during April, 2007 (15±7 kg h<sup>-1</sup>) and February, 2007 (15 $\pm$ 3 kg h<sup>-1</sup>; Fig. 4). Year-wise comparisons revealed that catch rates were higher during February – April 2006 followed by February – April, 2008 and February – April, 2007 (Fig. 4).

#### **Pufferfish catches**

The Half-smooth golden pufferfish *Lagocephalus* spadiceus (Richardson, 1845) was observed to contribute 0 - 27 % by weight of the trawl hauls during the present study (Fig. 3). The highest mean catch rates

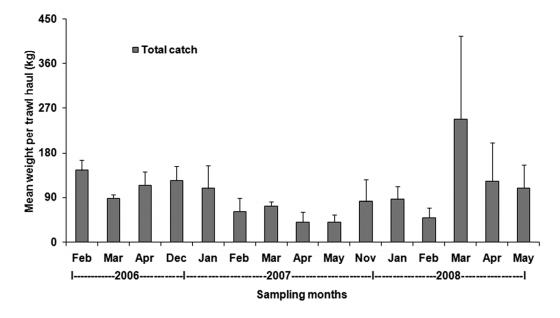


Fig. 2 — Month-wise trends of demersal fish (total catch) hauled by shrimp trawler off Goa

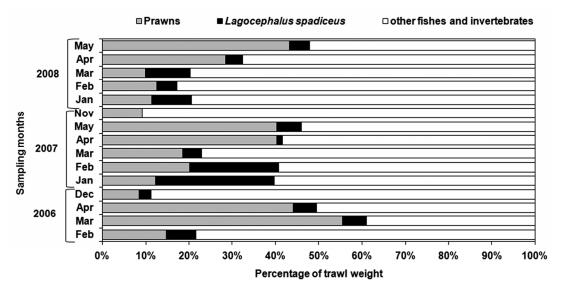


Fig. 3 — Month-wise percentage contribution of prawns (target organisms), the pufferfish Lagocephalus spadiceus, and other fishes and invertebrates to total trawl catches

of this species were observed during March, 2008  $(49\pm35 \text{ kg h}^{-1})$  and the lowest during November, 2007 (0 kg h<sup>-1</sup>) (Fig. 4). Year-wise comparisons revealed higher catch rates during February – April, 2008, followed by February – April, 2007 and February – April, 2006 (Fig. 4).

# Other fish and invertebrate catches

199 by-catch species viz. elasmobranchs, teleosts including *L. spadiceus*, stomatopods, crabs, molluscs, echinoderms, sea snakes and jellyfishes were observed in the trawl hauls. Their catch data (except *L. spadiceus*)

were pooled together as "Other fishes and invertebrates", and month-wise assessment revealed that this group contributed 39 - 91 % to the total catches (Fig. 3).

# Discussion

Mechanized Otter Board Motor (O.B.M.) trawlers are commonly employed to efficiently harvest enormous quantities of marine groundfish and invertebrates<sup>22</sup>. Mechanized fishing in the Goan waters commenced during the 1960's, expanded rapidly over the next thirty years and resulted in surpassing the Maximum

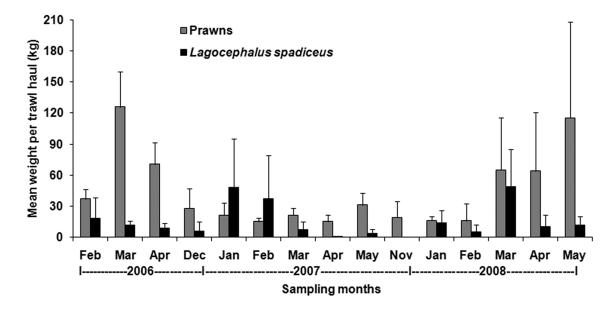


Fig. 4 — Month-wise catch trends of prawns (target organisms) and the pufferfish Lagocephalus spadiceus

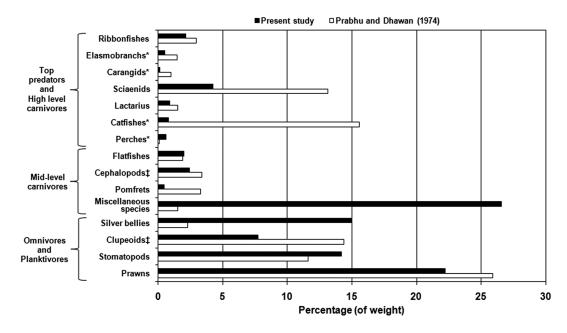


Fig. 5 — Species composition of demersal trawl catches off Goa coast – a comparison with Prabhu and Dhawan (1974). Star symbol (\*) indicated predators of puffers; Double dagger (‡) indicates prey organisms of puffers

Sustainable Yield (MSY) due to intensive fishing activity for lucrative species<sup>6</sup>. Despite this, published literature on the species composition of bottom trawlers operating in the near-shore regions of Goa is scanty<sup>11</sup>. Hence, intensive sampling was carried out to determine the trawl catch species composition and compare with published data to assess the impact of trawling on the epifaunal community structure of the near-shore fishing grounds off Goa.

The present assessment of trawl species composition and comparison with published literature<sup>11</sup> revealed considerable reduction in the percentage of top predators and high-level carnivores (elasmobranchs, carangids, sciaenids, catfishes) and mid-level carnivores (pomfrets) (Fig. 5). On the other hand, there was a manifold increase in low-valued bycatch comprising "Miscellaneous species" (Fig. 5), particularly due to the conspicuously large quantities of the pufferfish

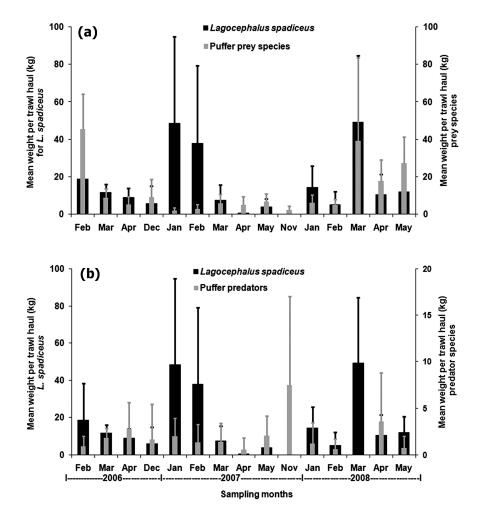


Fig. 6 — Month-wise catch trends of (a) Lagocephalus spadiceus and puffer prey species, (b) Lagocephalus spadiceus and puffer predators

*Lagocephalus spadiceus*. This species was observed to be highly abundant during January – February, 2007, January, 2008 and March, 2008.

Lagocephalus spadiceus is a demersal species<sup>12</sup> inhabiting sandy substrates in shallow coastal waters of less than 50 m depth, and entering estuaries  $^{23,24}$ . It is known to be a mid-level carnivore preying upon fishes, crustaceans and cephalopod molluscs<sup>25</sup>. Its predators include wide-mouthed carnivores such as sharks, cobia and catfishes<sup>26</sup>. This species is known to attain sexual maturity at 9 cm Standard Length (SL), breeds during February - March and September -November along the adjacent Maharashtra coast<sup>25</sup> and prefers sub-tidal rocky areas for spawning<sup>27</sup>. This species also exhibits voracious feeding behavior during the peak breeding season<sup>25</sup>. Against this background, the increased pufferfish abundance observed during January - February, 2007, and March, 2008 suggests that this species migrates to

near-shore coastal waters for breeding or spawning purpose. Further observation revealed that the L. spadiceus specimens collected during these sampling months were larger than 9 cm SL suggesting that much of the population comprised of sexually mature adults. On-field observations revealed that the fishing grounds in the study area are bordered with numerous sub-tidal rocky patches and promontories near the mouth of the Mandovi estuary. These rocky patches probably offer suitable substrate for spawning. Moreover, these near-shore areas support abundant quantities of prey organisms such as anchovies, squids and cuttlefishes. An assessment of the month-wise pooled catch data of prey species revealed that their catches were considerably lesser than L. spadiceus during January - February, 2007, and January, 2008 (Fig. 6a). These observations suggested that L. spadiceus could feed intensively during its peak breeding season. However, its absence

from the trawl catches during November 2007, which is known to coincide with a secondary peak in breeding activity<sup>25</sup>, necessitates further investigation to validate the observation. Intensive mechanized fishing activity in this region has resulted in the increased removal of puffer predators such as sharks, cobia and catfishes. An assessment of month-wise pooled catch data of predator species revealed that their catches were considerably lesser than *L. spadiceus* during February, 2006, January – February, 2007, and January, 2008, March, 2008 and May, 2008 (Fig. 6b). These observations suggested that reduction in predator populations has arguably reduced predation pressure, thereby facilitating proliferation of the *L. spadiceus* population in the study area.

Validation of correlation between catches of *L. spadiceus* on one hand, and its prey species and predators on the other using regression analysis revealed insignificant negative correlations between them (Fig. 7a, b). This discrepancy in the correlation between *L. spadiceus* and prey species/ predators

could be explained by variations in trophic transfer efficiency of various levels in a food chain. Trophic transfer efficiency is a function of prey-predator body size relationships<sup>28</sup>, foraging<sup>29</sup>, proportion of nitrogen in food<sup>30</sup> and proportion of energy lost through respiration<sup>31</sup>. Ware<sup>32</sup> estimated that in most marine ecosystems, trophic transfer efficiency ranged from 10 - 20 %. For example, to grow 1 kg of biomass, a predatory catfish or shark may require approximately 5 - 10 kg of pufferfish to sustain growth, which in turn would require up to 100 kg of prey species biomass. However, most coastal marine ecosystems are heavily exploited resulting in higher rate of fishing-related mortality as compared to predationrelated mortality<sup>33</sup>. Therefore, the trophic efficiency estimates are erroneously estimated.

Recent trends in CMFRI landing data (1982 – 2004) for sharks and other carangids (including the cobia *Rachycentron canadum*) suggested that increased demand has resulted in their removal in significant quantities<sup>19</sup> (Fig. 8a, c). On the other hand,

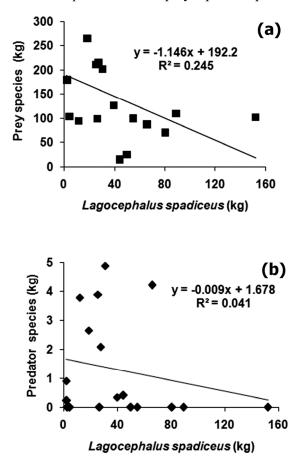


Fig. 7 — Regression analysis between (a) *L. spadiceus* and prey species, (b) *L. spadiceus* and predator species

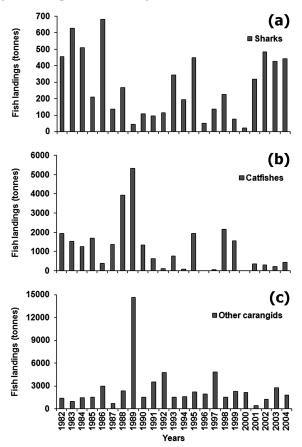


Fig. 8 — CMFRI fish landing data of potential puffer predators namely (a) sharks, (b) catfishes, and (c) other carangids during 1982–2004.

data for catfishes suggest that their catches are dwindling<sup>19</sup> (Fig. 8b). Analysis of marine fish landing trends obtained from the Directorate of Fisheries, Government of Goa for the period from 2000 - 2012 indicated a marginal reduction in shark landings during this period, whereas those of catfishes exhibited an oscillating pattern (Fig. 9a, b). The catch trends of catfishes exhibited a decreasing trend from 2006 - 2008, which corroborates our observations during the above period (Fig. 9b).

Comparison of CMFRI and Directorate of Fisheries data sets for the overlapping period from 2000 - 2004 revealed that catch figures differed substantially between them. It is essential to note that CMFRI and the State Fisheries Department follow different methodologies to estimate fish landings. The CMFRI employs a stratified multi-stage random sampling technique that involves recording fish landings from randomly selected major fishing harbours along the pre-selected zones<sup>34</sup>. The sampling duration is determined by segregating a month into three groups of 10 days each, followed by randomly selecting five days from each 10-day group while maintaining an interval of 10 days between each group. Moreover, recording of entire catches of all fishing boats landed at a particular harbour is done only if their total number is less than 15. However, if the total number

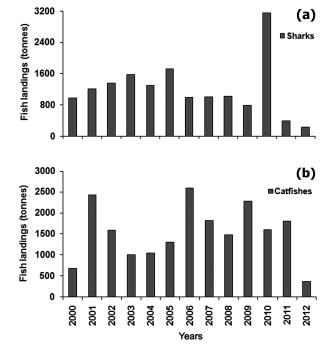


Fig. 9 — Fish landing data of potential puffer predators namely (a) sharks and (b) catfishes during 2000–2012 (Courtesy: Directorate of Fisheries, Government of Goa, 2012–13)

of boats exceeds 15, then recording of catches is carried out only for a pre-determined fraction of the total number of boats. Data comprising of species, weight, fishing vessel and gear is analyzed using INDFISH software to facilitate estimation of marine fish production<sup>33</sup>. On the other hand, the fishery data enumeration by the Directorate of Fisheries involved daily recording of entire catches of all the marine fishing vessels landed at each jetty along the state, followed by categorization of the catch into major species and type of fishing gear. In view of above differences in sampling design employed by these institutions, it is essential to exercise caution while using such data sets to infer the status of marine fisheries of the region.

Proliferation of L. spadiceus is a clear indication of alteration of demersal fish community structure, which may be aggravated due to its voracious feeding behavior<sup>25</sup>. Moreover, this species possesses sharp plate-like teeth capable of destroying most types of nylon fishing nets due to which it is considered a nuisance by artisanal shore seine fishers along the adjacent Maharashtra coast<sup>27</sup>. Similar proliferation of another congeneric species namely Lagocephalus inermis (Temminck & Schlegel, 1850) since 2006 along the Kerala coast has resulted in significant economic losses to mechanized trawl fishers<sup>26</sup>. These recent events suggest that intensive mechanized fishing has altered the marine epibenthic (or demersal) community structure by removing top predators and facilitated the proliferation of smaller predators, known as "meso-predator release"<sup>35</sup>. The above phenomenon would result in the removal of mid-level carnivores (anchovies, squids and cuttlefishes) by the meso-predator puffer, and turning it into a planktivore dominated ecosystem. This phenomenon, popularly termed as "trophic cascade" would lead to decrease in the zooplankton population, thereby facilitating unrestrained growth of the phytoplankton biomass<sup>36</sup>. Excessive phytoplankton growth is facilitated in the coastal regions by anthropogenic nutrient enrichment and might result in blooms of harmful algal species<sup>37</sup>. Harmful algal blooms are extremely hazardous for demersal fish and shellfish resources leading to large fish kills<sup>38</sup> as well as Paralytic Shellfish Poisoning (PSP) in humans<sup>37</sup>.

#### Conclusion

The present study reveals that the indiscriminate removal of HTL species results in the proliferation of the pufferfish *Lagocephalus spadiceus* (a mesopredator) which has potential implications for the commercial mechanized trawl fishery of the region.

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## **Conflict of Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

# **Author Contributions**

VPP: Conceptualization, formal analysis, methodology, writing. AC: Formal analysis, validation, writing. CUR: Conceptualization, formal analysis, funding acquisition, investigation, project administration, resources, supervision, writing original draft, review & editing.

#### References

- 1 Thrush S F & Dayton P K, Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity, *Annu Rev Ecol Syst*, 33 (2002) 449–473. https://doi.org/10.1146/annurev.ecolsys.33.010802.150.515
- 2 Islam M S & Tanaka M, Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis, *Mar Pollut Bull*, 48 (7–8) (2004) 624–649. https://doi.org/ 10.1016/j.marpolbul.2003.12.004
- 3 Ansari Z A, Chatterji A, Ingole B S, Sreepada R A, Rivonker C U, et al., Community Structure and seasonal Variation of an Inshore Demersal Fish Community at Goa, West Coast of India, Estuar Coast Shelf Sci, 41 (1995) 593–610. https://doi.org/10.1016/0272-7714(95)90029-2
- 4 Anil A C, Venkat K, Sawant S S, Dileepkumar M, Dhargalkar V K, *et al.*, Marine bioinvasion: Concern for ecology and shipping, *Curr Sci*, 83 (3) (2002) 214–218.
- 5 Rodrigues V, Ramaiah N, Kakti S & Samant D, Long-term variations in abundance and distribution of sewage pollution indicator and human pathogenic bacteria along the central west coast of India, *Ecol Indic*, 11 (2) (2011) 318–327. https://doi.org/10.1016/j.ecolind.2010.05.010
- 6 Ansari Z A, Achuthankutty C T & Dalal S G, Overexploitation of fishery resources, with particular reference to Goa, In: *Multiple dimensions of global environmental change*, edited by S Sonak, (TERI Press, New Delhi), 2006, pp. 285–299.
- 7 Padate V P, Biodiversity of demersal fish along the estuarine shelf regions of Goa, Ph.D. thesis, Goa University, Goa, 2010

- 8 Hegde M R, Padate V P, Velip D T & Rivonker C U, An updated inventory of new records of macrofauna along Goa, west coast of India, *Indian J Geo-Mar Sci*, 42 (7) (2013) 898–902.
- 9 Qasim S Z, *Indian Estuaries*, (Allied Publication Pvt. Ltd., Mumbai), 2003, pp. 259.
- 10 Padate V P, Rivonker C U & Anil A C, A note on the occurrence of reef inhabiting, red-bellied yellow tail fusilier, *Caesio cuning* from outside known geographical array, *Mar Biodivers Rec*, e3 (21) (2010) 1–6. https://doi.org/10.1017/ S1755267210000151
- 11 Prabhu M S & Dhawan R M, Marine Fisheries Resources in the 20 and 40 metre regions off the Goa Coast, *Indian J Fish*, 21 (1) (1974) 40–53.
- 12 Froese R & Pauly D (eds.) *FishBase*, World Wide Web electronic publication. http://www.fishbase.org version (12/2012).
- 13 Chhapgar B F, On the marine crabs (Decapoda: Brachyura) of Bombay State. Part I, *J Bombay Nat Hist Soc*, 54 (1957) 399–439.
- 14 Roper C F E, Sweeney M J & Nauen C E, Cephalopods of the World – An annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis No. 125, Volume 3. FAO species identification catalogue Volume 3, (Food and Agricultural Organization, Rome), 1984, pag var
- 15 Chan T Y, Shrimps and Prawns, In: FAO species identification sheets for fishery purposes. The Living Marine Resources of the Western Central Pacific, Vol 2, edited by K E Carpenter & V H Niem, (Food and Agricultural Organization, Rome), 1998, pp. 851–972.
- 16 Manning R B, Stomatopods, In: FAO species identification sheets for fishery purposes. The Living Marine Resources of the Western Central Pacific, Vol 2, edited by K E Carpenter & V H Niem, (Food and Agricultural Organization, Rome), 1998, pp. 827–849.
- 17 George M J, Subbaraju G & Dharmaraja S K, Trends in marine fish production in India 1982–83, *Mar Fish Inf Serv Tech Ext Ser*, 52 (1983) 1–21.
- 18 Mathew K J, David Raj I & Vincent D, Marine fish production in India during 1983–84 and 1984–85, *Mar Fish Inf Serv Tech Ext Ser*, 67 (1986) 1–79.
- 19 Srinath M, Kuriakose S, Ammini P L, Prasad C J, Ramani K, et al., Marine Fish Landings in India 1985–2004, CMFRI Spl Publ, 89 (2006) 1–161.
- 20 Sreekanth G B, Manju Lekshmi N & Singh N P, Catch trends in major marine fisheries resources of Goa. Technical Bulletin No. 49, (ICAR-ICAR Research Complex for Goa, Indian Council of Agricultural Research, Ela, Old Goa, Goa, India), 2015.
- 21 Bhathal B & Pauly D, 'Fishing down marine food webs' and spatial expansion of coastal fisheries in India, 1950–2000, *Fish Res*, 91 (2008) 26–34. https://doi.org/10.1016/ j.fishres.2007.10.022
- 22 Srinath M, An Appraisal of the Exploited Marine Fishery Resources of India, In: Status of Exploited Marine Fishery Resources of India, edited by M Mohan Joseph & A A Jayaprakash, (CMFRI, Cochin), 2003.
- 23 Talwar P K & Jhingran A G, *Inland fishes of India and adjacent countries 2*, (Oxford & I B H Pub Co Pvt Ltd, New Delhi, Bombay, Calcutta), 1991, pp. 616.

- 24 Tuncer S, Cihangir H A & Bilecenoglu M, First record of the Lessepsian migrant *Lagocephalus spadiceus* (Tetraodontidae) in the Sea of Marmara, *Cybium*, 32 (4) (2008) 347–348. https://doi.org/10.26028/cybium/2009-324-010
- 25 Naik S D & Jalihal D R, Biological observations on the pufferfishes of south Konkan coast with special reference to the net-damaging species *Lagocephalus spadiceus* (Osteichthyes, Tetraodontidae), *Indian J Geo-Mar Sci*, 27 (3–4) (1998) 426–432.
- 26 Mohamed K S, Sathianandan T V, Kripa V & Zacharia P U, Puffer fish menace in Kerala: a case of decline in predatory control in the southeastern Arabian Sea, *Curr Sci*, 104 (4) (2013) 426–429.
- 27 Naik S D, Observations on large-scale destruction of fishing gear by the pufferfishes (family Tetraodontidae) along the south Konkan coast (west coast of India), *Indian J Geo-Mar Sci*, 27 (3–4) (1998) 421–425.
- 28 Barnes C, Maxwell D, Reuman D C & Jennings S, Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency, *Ecology*, 91 (1) (2010) 222–232. https://doi.org/ 10.1890/08-2061.1
- 29 Anderson K H, Beyer J E & Lundberg P, Trophic and individual efficiencies of size-structured communities, *Proc R Soc B, Biol Sci*, 276 (1654) (2009) 109–114. https://doi.org/ 10.1098/rspb.2008.0951
- 30 Jennings S, Maxwell T A D, Schratzberger M & Milligan S P, Body-size dependant temporal variations in nitrogen stable isotope ratios in food webs, *Mar Ecol Prog Ser*, 370 (2008) 199–206. https://doi.org/10.3354/ meps07653

- 31 Lindeman R L, The trophic-dynamic aspect of ecology, Bull Math Biol, 53 (1–2) (1991) 167–191. https://doi.org/ 10.1016/S0092-8240(05)80045-X
- 32 Ware D M, Aquatic ecosystems: properties and models, In: Fisheries Oceanography: An integrative approach to fisheries ecology and management, edited by P J Harrison & T R Parsons, Fish and Aquatic Resources Series, (Blackwell Science, Oxford), 2000, pp. 160–194.
- 33 Rice J & Gislason H, Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblages, *ICES J Mar Sci*, 53 (1996) 1214–1225. https://doi.org/ 10.1006/jmsc.1996.0146
- 34 Srinath M, Kuriakose S & Mini K G, Methodology for the estimation of marine fish landings in India, *CMFRI Spl Publ*, 86 (2005) 1–57.
- 35 Eriksson B K, Sieben K, Eklöf J, Ljunggren R, Olsson J, et al., Effects of altered offshore food webs on coastal ecosystems emphasize the need for cross-ecosystem management, *Ambio*, 40 (7) (2011) 786–797. https://doi.org/10.1007/s13280-011-0158-0
- 36 Baum J K & Worm B, Cascading top-down effects of changing oceanic predator abundances, J Anim Ecol, 78 (2009) 699–714. https://doi.org/10.1111/j.1365-2656.2009. 01531.x
- 37 Trainer V L, Eberhart B -T L, Wekell J C, Adams N G, Hanson L, et al., Paralytic shellfish toxins in Puget Sound, Washington State, J Shellfish Res, 22 (2003) 213–223.
- 38 Azanza R V, Fukuyo Y, Yap L G & Takayama H, Prorocentrum minimum blooms and its possible link to a massive fish kill in Bolinao, Pangasinan, Northern Philippines, Harmful Algae, 4 (2005) 519–524. https://doi.org/10.1016/j.hal.2004.08.006