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WATERBIRD-MEDIATED CHANCE-DISPERSAL OF FISHES : A NATURAL PROCESS AFFECTING RANGE OF DISTRIBUTION AND BIOGEOGRAPHY OF FISHES

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INTRODUCTION

Many biogeographers have reported from time to time instances of waterbird-mediated dispersal of organisms, often speculating on this phenomenon enhancing the natural distribution of plants and animals (Darwin, 1859; Ridley, 1930; Proctor, 1959).

Waterbirds are considered passive dispersers of the propagules of aquatic invertebrates, by transporting them, either internally (through gut contents) or externally (adhered to feet and feathers), thus facilitating dual means of dispersal : internal dispersal or endozoochory and external dispersal or ectozoochory (Darwin, 1859; Proctor *et al*., 1967). Evidences on dispersal of amphipod crustaceans, through internal transport, by waterfowl have come from the studies of Daborn (1976) and Swanson (1984). Maguire (1963) has reported the waterbird-aided transport of aquatic organisms, which adhere to the plumage of birds, thus facilitating their passive dispersal and colonization in isolated water bodies. Through one experimental study, Segerstrale (1954) established that the amphipod *Gammarus lacustris* (Sars) adhered to plumage of a duck could retain its hold for over 2 hours. Vagvolgyi (1975) has documented instances of small snails found attached to bird feathers, getting dispersed to far away habitats.

Species enjoying wide distribution may comprise either morphologically similar complexes of sibling species or widely distributed conspecifics. Whatsoever, the wider distribution of species is indicative of their inherent ability and potential for getting dispersed, and make possible the gene flow from one area of distribution to another (Bohonak, 1999). Indirect evidences supporting the long distance dispersal of organisms by waterbirds have come from the studies of genetic populations of far-flung placed aquatic invertebrates, which reveal that the geographical distance between the

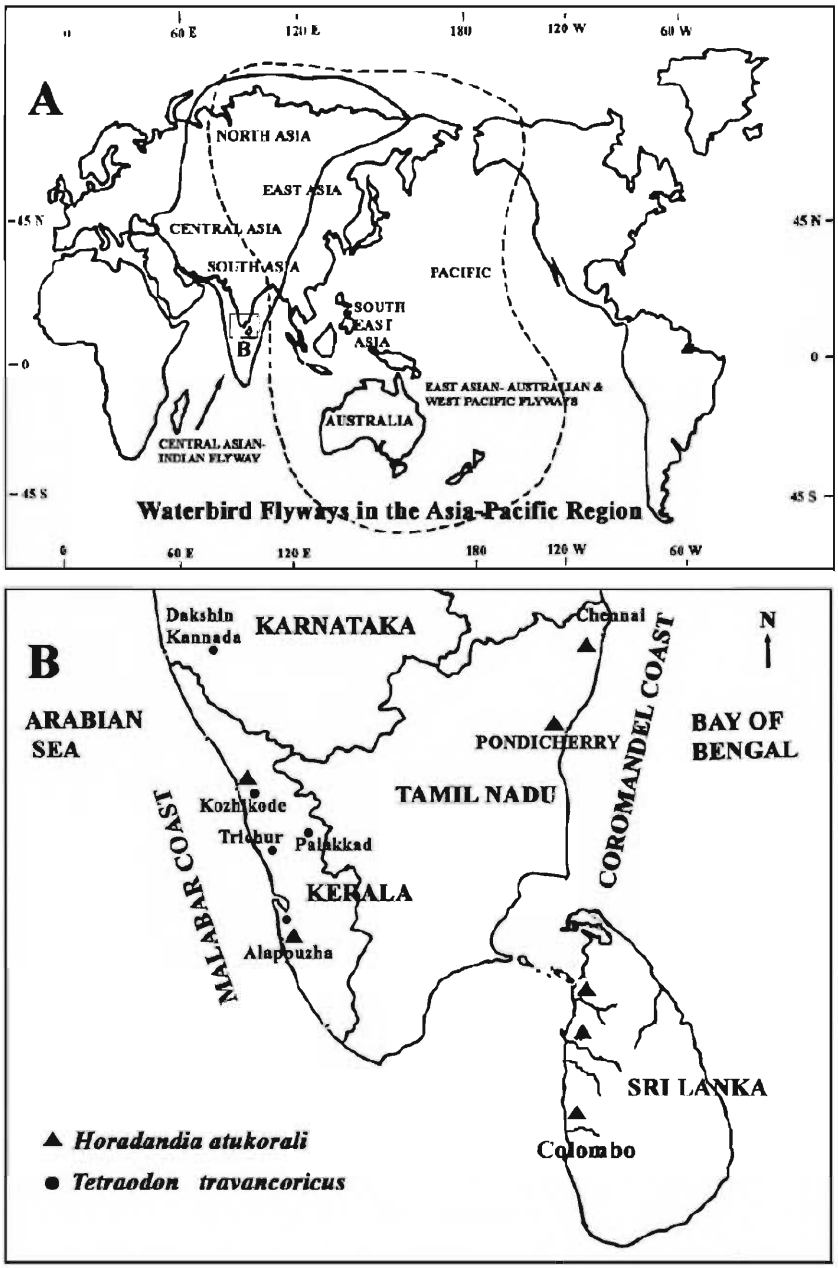

Fig. 1. : Link between the waterbird flyways and waterbird-mediated chance dispersal of prey fishes.

A. The waterbird-mediated chance dispersal events probably follow forage movements of waterbirds in a North Ö South direction of their flyway (Central Asian-Indian Flyway).

B. Extension of ranges of distribution of fish species : *H. atukorali* and *T. travancoricus*, in south India, probably aided by waterbird-mediated chance dispersal (distribution follows in a South Ö North direction of long/short distance forage movements of birds).

sub-populations is normally not related to their genetic distance (Freeland *et al.*, 2000a). The patterns of genetic distribution and biogeography of certain widespread freshwater invertebrates have been observed to follow the direction of major waterfowl flyways (Freeland *et al.*, 2000b; Taylor *et al.*, 1998).

Though waterbird-mediated dispersal of aquatic organisms is a frequently occurring phenomenon in nature, its relevance to the dispersal of fishes is seldom addressed and documented. Its significance remains apparently underestimated even while realizing that fishes, like aquatic invertebrates, constitute an important diet-component of waterfowl, particularly of piscivorous ones. Peterka (1989) has pointed out the possibility of freshwater systems getting stocked with fish-eggs or fry by waterbird-mediated dispersal, thereby enhancing the productivity of the systems. The relative importance of the waterbird-mediated dispersal of certain fish species, in comparison with distributional patterns of isolated populations of species offered by other competing means (Rosen, 1978; McDowall, 1978), has not been properly evaluated, probably due to lack of adequate supporting evidences.

This paper discusses some observations based on field studies on the possible passive dispersal of freshwater fishes by waterbirds, emphasizing its zoogeographic significance in the extension of range of distribution of fishes.

METHODOLOGY

In the present study, we have recorded some cases of the life of small fresh water fish species in odd aquatic habitat environs. These are illustrated as location-specific field observations. In this context, we have also considered the dispersal trends of the illustrated fish species from literature while linking up the case study observations on them, in order to derive at a conclusion with logical reasoning.

Field Observations :

Case study I

'Madaipara' in Kannur District, Kerala (India), is very characteristic for its lateritic plateau-land of about 600 hectares, abruptly raised to an elevation of 40 meters. Overlooking from the plateau top is the vast floodplains of the Kuppam River in the neighbouring Ezhome village in the coastal plains of the district.

During a field survey of this tableland, we observed small assemblages of freshwater fishes of two species, *Puntius vittatus* Day and *Aplocheilus blocki* (Arnold), thriving in two small pools in the plateau. It was a puzzle as to how these two fish species, in small populations, got established in the pools formed during the monsoon period. The plateau's topography naturally prevented the chance-immigration of these species in to the pools from other water bodies. After the rainy season,

the pools gradually dried up by November-December. Our regular observations revealed that prior to the drying up of the pools, waterbirds, such as pond-herons and egrets, preyed on the fish-stock of the pools.

The pools got replenished by the succeeding southwest monsoon rains (June to August), and initially there was no fish life in them. We also noticed some of the water birds, especially pond herons and egrets, occasionally frequenting the water pools. It was observed that waterfowl often with mud-stuck feet and soiled feathers used the pools for preening and cleaning activities. It was indicative of the birds' arrival from the foraging ground, presumably after feeding.

As happened in the previous year, the fish life revived in the pools, initially with the species *P. vittatus*, and then with *A. blocki*. The small fish population, hardly about 100 individuals comprising both the species, thrived in the pools till October-November, but again succumbed to predation by waterbirds, once the pools started drying up.

We observed this phenomenon recurring in the succeeding seasons also, which was monitored for three-more years (from 1998 to 2000). The small fish population temporarily established in the pools, observed during one visit in November 2005, also contained a few individuals of *Puntius ticto* and *Pseudosphromenus cupanus*, yet other two small forage fishes of waterfowl.

The fish species sighted in plateau-pools have some unique attributes, such as, smaller size, short breeding cycles, and high fecundity and reproductive potential than most of the other freshwater fishes. They are sought after by waterbirds owing to their ubiquitous presence in almost all freshwater habitats.

The inference from our observations is that the fish life in the tableland pools was seasonally influenced and enhanced by the visits of the waterfowl.

Case study II

Another interesting case of distribution of a fish is that of *Horadandia atukorali* Deraniyagala, reported from the freshwater bodies in the coastal plains of Kerala, Tamil Nadu and Pondicherry in South India. *H. atukorali*, a small carp-let about 3 cm long, was earlier thought to be endemic to Sri Lanka, until Rema Devi and Menon (1992) reported it from a pond in the Pathiramanal Island in the Vembanad Lake in Southern Kerala. Later, it was reported from Kumarakom (Rema Devi *et al.*, 1996) close to the Vembanad Lake, and also from Kalpakkam near Chennai (Tamil Nadu) and Villianur (Pondicherry) along the East Coast (Rema Devi, 1996).

H. atukorali is a prolific breeder whose eggs, remaining attached to submerged weeds, hatch in 36-48 hours, and its life cycle is so compressed that the reproductive life of this fish is over in a year (Brittan, 1961). In its original habitat in Sri Lanka, the species is a still or slow swimming fish, frequenting less saline mangrove swamps and less polluted canals, rice fields and similar waters, wherein its population increases to noticeable proportion (Pethyagoda, 1991).

It was quite intriguing to find *H. atukorali* along with three other small species of fishes, in a recent collection from the freshwater tank, Mananchira, in the Calicut City, North Kerala (Gopi *et al.*, 2004b). The tank with an area of 100 sq. m is well protected on all sides, and since the 1980s has been in use as the main drinking water-supply source of the city. Prior to starting the water supply scheme, this old tank had been thoroughly revamped by deepening and draining out processes, and sanitation works. Obviously there was little chance for the occurrence of any characteristic biota such as fish in the tank, at least in the beginning. Hence, the occurrence of fishes in the tank at present, as evidenced by our recent fish-collection, calls for an explanation since our attempts at collecting fishes from the tank, for a few years in the past, had not yielded any positive results.

The fish collection from the waters of the tank (on 6.1.2003) comprised of the freshwater species, *H. atukorali, A. blocki, P. vittatus* and *P. cupanus.* All these four species were in moderate abundance in the tank waters, amidst the grassy weeds. The fish community of the tank consisted only of small fish species, notably *H. atukorali.* It was also observed that piscivorous waterbirds like Little Cormorant (*Phalacrocorax niger*), Little Grebe (*Podiceps ruficollis*), Little Egret (*Egretta garzetta*), Median Egret (*Egretta intermedia*) and Pond Heron (*Ardeola grayii*) frequented the tank waters in good number. Hence it is inferred that these fish species have in all probability been passively dispersed to the tank environs by the piscivorous waterbirds that usually frequent the freshwater habitats in search of feeding grounds.

Case study III

The Malabar Pufferfish, *Tetraodon travancoricus* Hora & Nair, is a small species about 2-3 cm long, described from the Pamba River system that empties into the Vembanad Lake. Since the description of this species in 1941, it remained elusive for nearly four decades, hence deriving it the status as a rare/vulnerable species. There has been no record of this fish from any other habitat till 1993 when Inasu (1993) collected the fish-samples during May, June and September (1992), from the inundated brickyards at Pudukkad, Trichur, Kerala, and later Biju, *et al.*, (1999) made their collections, during the summer months (January to May), from the fresh water bodies at localities : Thattekad and Kalady of Periyar River, Kanakkankadavu of Chalakudy River and Puzhakkal of Ketchery River. Further, Rema Devi *et al*., (1996) identified this species from Kerala, and the specimens of *T. travancoricus* in the samples hold the data of the collection-sites as : “a ditch near Kottayam Railway Station” (5 exs., Dec., ’87), “Minachil River, Kottayam” (2exs., 5.12.1987) and “Pathiramanal Island (pond), Vembanad Lake” (1 ex., 7.4.90). Based on these specimens in the fish collection, Ahlander (1998) has also reported the distribution of this species along the coastal belts in southern Kerala.

During a faunal exploration of Alappuzha District in South Kerala in April-May, 2004, many dozens of specimens of the Malabar Pufferfish *T. travancoricus* were collected from Thavanakadavu,

near Cherthala. The collection-site, the mouth of a small stream-inflow-creek with very shallow waters, littered with floating duckweeds, harboured this pufferfish population in great abundance. The association of this species with the duckweeds offering shade and shelter was very conspicuous. It was also observed that waterfowl, in good number, foraging in shallow waters also joined the puffer fish population as an integral component of the habitat site.

We could collect this species, during the summer months (2003), from a waterpool in the almost dried up Kalpathypuzha tributory of the Bharathapuzha River in Palakkad District. From northern Kerala, Shaji and Easa (1998) have reported this "vulnerable" species in the upland river habitats of the Chaliyar drainage system. We have noticed this puffer fish in our sample collections from the freshwater bodies, including the irrigation channels in the coastal plains, associated with the Chaliyar River. But, from the river systems of Kerala north of Chaliyar River, this puffer fish has not so far been reported.

The distribution of *T. travancoricus* became more interesting when Rema Devi *et al.*, (2000) reported these tiny tetraodontids from the aquatic environs of the evergreen forests, around Mavincar, Dakshin Kannada, at 50 m above MSL, indicating the extension of its range of distribution to Karnataka. It indicates a dispersal trend for the species towards northern geographical ranges, irrespective of its population-distribution being earlier reported only from the riverine-brackishwater habitat systems of Kerala. The earlier assessed rarity status of this species is in conflict with its current well-dispersed status based on its known range of distribution and abundance. All the recorded cases of extension of range of distribution of this species seem to have resulted by subsequent dispersal events.

A notable observation is the ubiquitous association of the waterbirds with the aquatic habitat environs, wherefrom this puffer fish has been reported. Thattekad is a recognized bird sanctuary in Kerala. The collection-localities in Trichur District are not too far off from the Kole wetland system, which is a well-known waterfowl habitat. Waterfowl community is an inseparable biotic component of the Vembanad Lake ecosystem, and the habitat areas like Pathiramanal Island surrounded by the lake waters, and Kumarakom, a waterfront beach-hamlet, are shelter-abodes for many nesting waterbirds.

Given the bionomics of this species, such as its reclusive, shade and shelter loving nature, and the slow-swimming movement, the occurrence of *T. travancoricus* in odd aquatic habitats/ microhabitats such as artificial tanks/abandoned water bodies in paddy fields, an isolated ditch (near Kottayam Railway Station), a pond in a small island (Pathiramanal island), a depleting water pool in an almost barren river bed (Kalpathypuzha) or upland aquatic environs amidst forested areas (Mavincar, Dakshin Kannada) are quite intriguing. It appears that the piscivorous birds tend to passively play a role in the dispersal of their prey species aiding in the extension of their range of distribution, probably employing mutualism.

Case study IV

The distribution of *Horaichthys setnai* Kulkarni, the smallest known fish, in India, about 2 cm long, generally known as Thready Killifish, is very characteristic. Primarily an estuarine form, also living temporarily in freshwaters, this tiny species inhabits the creeks of backwaters along the West Coast. Kulkarni (1940) described it from the backwaters and tanks along the West Coast (type locality, Navalaki, Kathiawar coast) of Mumbai. Far from its type locality, Job (1940) reported this species from the coastal backwaters of Cochin and Trivandrum (localities : Cheranellore and Mannummel). Considering the fluviatile nature of the species and the long stretching coastline of the West Coast, Job (1940) and Silas (1959) presumed the distribution of the species along the West Coast of India, from the Gulf of Kutch (Gujarat) to Trivandrum (Kerala), despite its populations exhibiting far-isolated distributional trends.

Karamchandani and Pandit (1971) located this species from Narmada River at Jhanor as far inland as 64 Km from sea, and from the freshwater sites of Tapti River, at Kathor and Bodhan, far interior from the sea, and noted the tendency of the fish to ascend the rivers to the freshwater zones. But, *H. setnai*, usually found in the puddles and pools of stagnant brackish waters, is a slow swimming species forming swarms near surface of water, mostly amidst aquatic plants (Jayaram, 1999). This species shows discontinuous distribution as evidenced from records.

The species has remained elusive even after exhaustive ichthyological collection efforts in Kerala (Shaji and Easa 2001), for more than three decades. However, the occurrence of this species, quite far away from the already known distributional areas of the coastal backwaters along the West Coast (South Kerala, Mumbai coast and Gulf of Kutch) was noticed by us, during August 2001, in the inundated paddy floodplains of Ezhome village, in Kannur District in northern Kerala. A habitat site serving as a natural sanctuary of this species, associated with a small island, namely, Thekkumbad was also located, during November 2001, in the estuarine waters of Kuppam River (Gopi, *et al.*, 2004a). The population of the Thready Killifish very well thrived in the shallow waters amidst the mangrove patch on the inundated mudflat of the island. During the seasonal flooding of the areas in monsoon period, they became ubiquitously present in dense populations in the adjoining floodplains within the island as well as in the floodplains of Ezhome. As the season's rain ebbed and the water level gradually receded, the entire floodplain areas of Ezhome and Thekkumbad Island, abound with the populations of prey-fish species (such as *H. setnai*, *P. vittatus*, *A. blocki*, besides many other species and aquatic invertebrates), became a habitat-zone of intense foraging activity of innumerable waterbirds. The discontinuous distribution of *H. setnai* in its known range appears to have been influenced by the waterbird-mediated dispersal processes.

DISCUSSION

In this field-oriented study highlighting the probable dispersal of fishes by waterbirds, we have concentrated on only a limited number of species, a few species of fish and some water-

birds feeding on them, to postulate some assumptions on waterbird-mediated chance dispersal of fishes.

Small forage fishes, unlike the larger forms, have higher reproductive potential, with shorter breeding cycles enabling them to build up their populations with minimum requirements of space and time. In ecological perspectives, these species have abundance in their number at any time of the year in their habitats, and such habitats are better foraging sites of waterbirds.

Waterbirds like herons and egrets prey upon fish and other aquatic organisms from the shallow, weed-infested or muddy margins of the inundated paddy fields, floodplains and other freshwater habitats, whereas cormorants, teals and dabchicks are capable of foraging from deep waters. It is likely that waterbirds while scouring the weeds or debris in the shallow margins or muddy edges of water bodies for their prey, like small fishes, the viscid egg masses of the prey species sheltered amidst water-weeds or in the vicinities, are sometimes dislodged and get adhered to the feet or body of the bird; it is a near certain possibility during breeding phase of the small prey fishes, when their fertilized ova or eggs are abundantly available in the habitat waters. The fish ova/seeds that accidentally get stuck to the body or mud-smeared-feet of a bird, get the chance to be carried while the bird moves from one habitat to another, thus passively dispersing the fish ova to the allied or new habitats.

Waterbird-mediated long/short distance dispersal of adult fishes, sub adults or fingerlings, may be unlikely, since the larger size of the dispersal material and its exposure to desiccation during long transport are likely to be limiting factors. But, the slimy fish ova or seeds are at an advantage, over fingerlings, with their better adaptability to resist desiccation and retain the viability for longer durations even after removal from water (Darwin, 1859). Bilton *et al*., (2001) have observed in the case of freshwater invertebrates that many seeds and resting eggs are likely to be highly resistant to desiccation.

The occurrence and establishment of populations of small fishes, such as *P. vittatus*, *H. attukorali*, *A. blocki*, *P. cupanus*, etc., in the Mananchira Tank waters (Calicut, Kerala), an almost refreshed system of a freshwater pond-habitat, can be surmised in the light of the feeding ecology of waterbirds that visit this pond system for foraging. As for the tiny carp-let *H. attukorali*, in the present study, the waterbird-mediated dispersal appears to offer a sound reason for its occurrence and establishment in a rejuvenated system, far away from its primarily and secondarily known home habitats (freshwater wet plains of Sri Lanka and South India, respectively). In the case of *H. attukorali*, or *T. travancoricus*, the populations currently exhibit discontinuity in the range of distribution with explicit geographic isolation. Despite this isolation factor, the sub populations from varied habitat zones are morphologically indistinguishable, i.e. they are having little inter-population differentiation, consistent with morphological similarity across the species' range, indicating an on-going gene flow between the populations. It is indirect evidence suggesting the distribution having followed

the waterbirds' flyways. Even if the lack of association between genetic and geographic distances in the populations does not serve as an evidence for bird-mediated dispersal, the other facts that the populations are not at equilibrium (at far-isolated locales) in the range of distribution, and that the naturalization/colonization events are independent of the geographical distances/barriers suggest that the dispersal trends are more frequent in the direction of birds' foraging movements, between stopover areas, during long or short distance flights.

This mode of dispersal seems to have greatly influenced the dispersal of small fish species, particularly the small, surface and sub-surface dwelling prey-fishes, to become, biogeographically, the widely distributed fishes. Such fishes, sometimes in striking colours, have small size, no pronounced growth of spines, and comparatively shorter breeding cycles, with high turn out of progenies, all of which suite to the advantages of the waterbirds preying on them.

Chance dispersals of fishes, passively by waterbirds, from their home-habitats to allied aquatic bodies elsewhere, at times, result in the extension of range of distribution of the species. It is understandable that the chance dispersal of species, over time, in a slow or frequent manner enables a species to 'skip' to new areas, slowly extending its range of distribution, sometimes marked with a discontinuity in the distributional pattern. It leads to the shuffling of the patterns of distribution within the range of occupation. As can be seen, the period of collection/observation of the fish species *H. attukorali* and *T. travancoricus* from varied locales, as reported by different workers, cited in the present study, coincides with the period of intense foraging activity of waterbirds.

The cypriniform fishes have become, in general, the dominant freshwater group in their known distributional range. In most places, the species of the small-sized cyprinoids are the principal forage fishes of waterbirds. The cyprinid fishes of the large speciose group, the genus *Puntius* (Cyprinidae) in the Oriental Region, for example, are widely distributed in South Asia. Most of them do not grow to large size, but compensate with their abundance, and have become important forage fishes. Biogeographically, how these small fishes (e.g. *P. vittatus*, *P. ticto*, *etc.*) happened to have their distribution in a very wider geographic range, across the Indian subcontinent? Our field observations on the small forage fish species, *P. vittatus*, *H. attukorali*, *H. setnai*, *A. blocki*, *P. cupanus* and *T. travancoricus*, associated with the piscivorous waterbirds, seem to suggest that these small forage fishes have been enjoying the advantage of the waterbird mediated dispersal in their biogeography and evolutionary progress. The principle of mutualism seems to have been in play in the feeding ecology and prey-predator relationship of waterbirds and prey-fishes. Thus there is compelling reason to consider that some cyprinoid fish-groups, like *Puntius*, exhibiting remarkable geographical radiation and great diversity in species in their evolutionary history, must have benefited by the waterbird mediated dispersal, thereby enjoying wider range of distribution and dominance.

The Little Cormorant from its earlier status as being a doubtless resident bird, with no record of breeding in Kerala, rose to the level, later, with a notable population distributed in the wetland

environs of southern Kerala, but till then seldom spread to northern Kerala and further north (Neelakantan, 1986). But, currently, they are among the very common species found in almost all available freshwater systems in the southern states (perhaps major part of the country, even), seen foraging from lowland floodplains and ponds to upland or highland water bodies like lakes, reservoirs and even the temporary aquatic habitats amidst the forest environment. Similarly, two other local resident waterbirds, the Pond heron and Little egret, also exhibit more vagrant, explorative feeding movements to the extent that, within their reasonable range of occupancy, no freshwater habitat system can be seen without their presence.

Given the facts that the long migratory journeys of many waterbirds follow the Central Asian-Indian Flyway in the Asia Pacific region (Fig. 1. A), the alignment of India and Sri Lanka in a North-South than an East-West direction, falling in the same migratory Flyway, and the tendency of many of the waterbirds following common flyway routes, to and fro, connecting both the countries for foraging purpose, it is likely that waterbirds while undertaking long or short distance movements in either direction may stop over at suitable aquatic habitats for foraging. Many migratory shorebirds make use of the foraging grounds of the coastal and inland wetlands like, jheels, inundated paddy fields, floodplains and even temporary or seasonal pools in the uplands of both the countries (India and Sri Lanka).

A migratory waterfowl from Sri Lanka carrying a few freshly gathered fish-ova/eggs (of *H. atukorali*, for example) from a fresh water habitat, accidentally trapped on its feet, or feather, can easily make a cross-over flight to the nearest, allied habitat in the west/east coastal plains in South India, which is only about 100 Km or less from Sri Lanka. As for ducks known to fly at speeds of 60-70 km/h, and waders at speeds 50-60 km/h, this distance can easily be covered in one and a half to two hours without affecting the viability of fish-propagules, in case they carry them as dispersal agents.

Another possibility is that the waterbird-mediated chance-dispersal of the prey-fish species usually occur at higher frequency levels, from an original or core habitat zone harbouring abundance of the prey-fish population to a near or distant allied aquatic habitat. The species propagules attaining their access to other habitat locales may successfully establish themselves in the new habitats, provided the conditions are suitable for their naturalization. It is therefore not the dearth of frequency of the waterbird-mediated dispersal of the species concerned, but the colonization/ naturalization process of the subpopulation that ultimately determines the success of its establishment in a new habitat. It seems to be a key reason why the trend of discontinuity in the extended range of distribution is reflected in the dispersal events of these species. The relative densities of populations of *H. atukorali*, with highest concentration in its prime center of occurrence, *i.e.*, Sri Lanka, and in lesser densities in the extended ranges of distribution in Kerala, Tamil Nadu and Pondicherry, are indicative of such selective naturalization in tune with natural selection.

Thus, it becomes evident that from the presently naturalized habitats in southern Kerala, or even from its original habitats in Sri Lanka, the same species has got access to the isolated tank system (Mananchira in Calicut district, Kerala) and to the fresh water wet plains of the east coast in Tamil Nadu and Pondicherry. The freshwater wet plains of the West Coast and East Coast of India despite having the formidable barrier of the Western Ghats System in between, the dispersal of this species has happened. The logical explanation is that the extension of range of distribution of this species might have taken place, through the waterbird-mediated chance dispersal. In similar modes, the extension of range of *Tetraodon travancoricus* seems to have also taken place along the west coastal freshwater habitats from southern Kerala to Karnataka (see, Fig. 1. B).

Our conclusion is that the waterbird-mediated passive dispersal of fish, particularly of prey-fish species of piscivorous waterbirds, is very probable in the freshwater habitats frequented by waterbirds, unless hampered by the adversities like excessive dispersal-delay or lack of viability of the dispersal propagules. Trends of wider distribution often exemplified by the small fish species are to a great extent indicative of the resultant causes and effects of waterbird-mediated species dispersals that have been taking place in natural aquatic habitat systems.

We have not considered one key factor here, that is, the adaptability of the bird-dispersed species to the new environment and its potential to compete with other species to establish itself in the new aquatic environment. It appears to be one key factor that causes the discontinuity of the distribution in the known wider range of these species.

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