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Diadromous Fish Extinction: Threats on Local and Global Scales (P)

Different kinds of diadromy: different kinds of conservation problems

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Abstract

This paper presents a world-wide review of the conservation status of diadromous fishes. In taxonomic and geographical terms, high levels of conservation threat are focussed particularly on sturgeons, family Acipenseridae, and on western/central Europe and the North Pacific. The geographical focus reflects largely the imperilled status of sturgeons rather than issues relating to species being diadromous. The paper also provides an interpretation of the threats to diadromous fishes, in terms of whether they are anadromous, catadromous or amphidromous. The significance of these varied forms of diadromy strategy is discussed in relation to the migration strategies that species adopt in moving to and from fresh water. About half known diadromous fishes are catadromous or amphidromous. Their patterns of migration and the ways they occupy river systems differ from those of anadromous fishes, and these fishes therefore require particular attention in providing for their conservation needs and in mitigating the effects of river management and modification.

Introduction

This paper addresses two distinct but interacting issues that relate to the conservation of diadromous fishes:

- Firstly it examines the broad spectrum of diadromous fishes to determine what species or groups of species are considered to be under conservation threat and whether there is any common feature about these species that might point to why they are threatened.
- Secondly, it looks at the different life history strategies exhibited amongst diadromous fishes, and points to specific issues that need attention with relation to their conservation.

In a sense, what I am doing is looking at a broad continuum of conservation issues in diadromous fishes from each of two opposing ends of that continuum, asking:

- What do diadromous species under conservation threat tell us about conservation in diadromous species? and
- What is there about diadromy in fishes that causes problems for their conservation?

In principle, it seems that diadromous fishes do have particular conservation problems that need to be addressed (McDowall 1992), but what does this mean in practice?

Diadromous fishes

In a broad review of diadromy, now about 10 years old (McDowall 1988), I found that nearly 230 fish species were then recognised as diadromous. Subsequent discoveries and taxonomic changes will have increased that number a little, but not greatly—perhaps to 250 species, or probably less than 1.5% of all known fishes. Diadromy encompasses three distinct migratory strategies, as defined by George Myers (1949) (see Fig. 1). Somewhat less than half the known diadromous species (48%) are anadromous, and a little more than a quarter each are catadromous and amphidromous. Changes in these numbers in the past decade are likely to have most affected numbers of amphidromous species, particularly as a result of the increasing recognition of the existence of amphidromy among the sicydiine gobies (Parenti & Maciolek 1993). In addition to fishes, there is a presently undocumented number of diadromous shrimps (families Atyidae and Palaemonidae) and gastropod molluscs (Family Neritidae) (Williams & Smith 1979; Resh et al. 1990; Schneider & Lyons 1993), all of which are amphidromous.

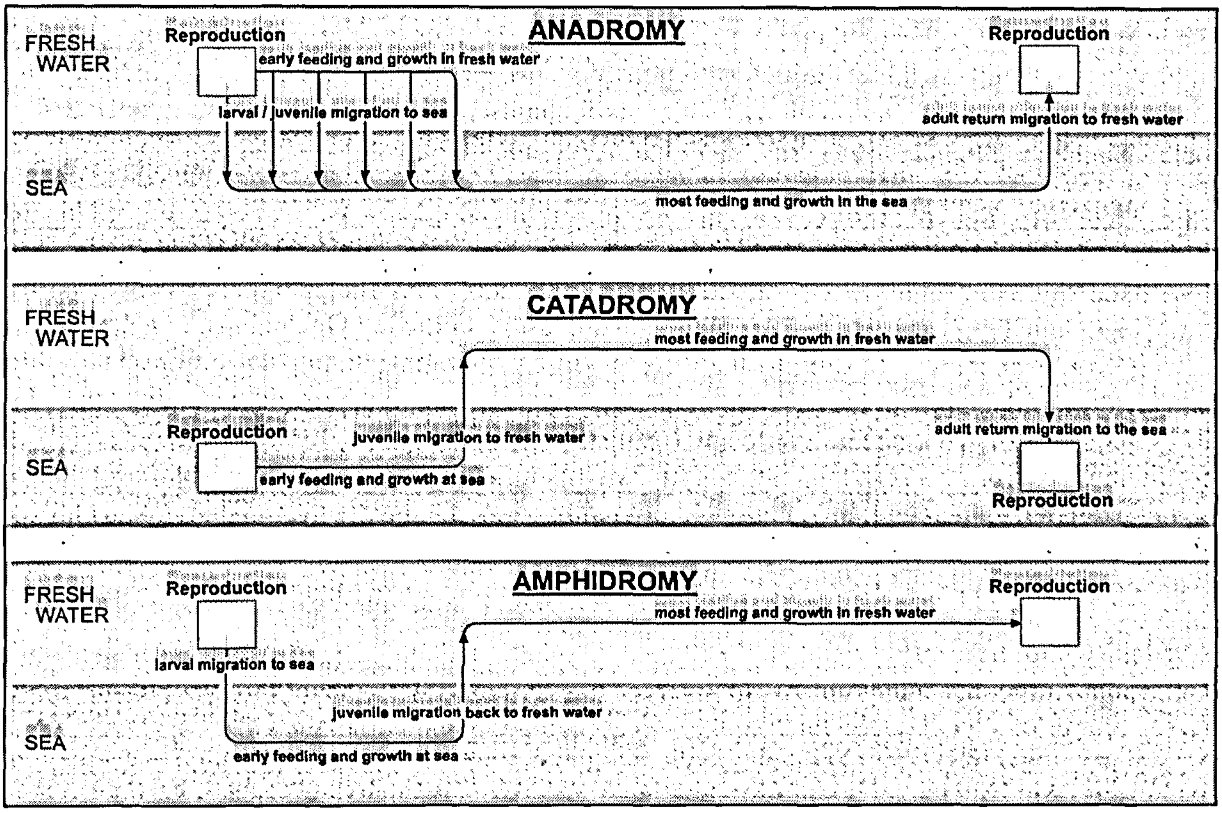

Fig. 1. Different kinds of diadromy

Thus, although diadromy is not exactly a major phenomenon in the world of aquatic life, nor is it a phenomenon to be "dismissed" as of little importance—a significant number of species is diadromous, and some of these are biologically, historically, or economically important or interesting. This, of course, explains why there is a specialist ICES committee on the subject, and why this meeting is being held.

This symposium's title relates to extinction in diadromous fishes, but clearly we need to view the subject a little more broadly than just extinction, to consider both actual and potential extinctions, of which the latter are the most important. This brings us face to face with diadromous species under some form of conservation threat. Conservation threat can be examined at geographical/taxonomic levels varying from:

- Species as a whole that are under threat, to:
- Threatened sub-species, races or evolutionarily significant units (Waples 1995).

Clearly, the much discussed issue with regard to conservation of northern Pacific salmonids (Nehlsen et al. 1991; Baker et al. 1996; Huntington et al. 1996; Slaney et al. 1996), brings into consideration detailed questions of catchment-adapted races, which I imagine will be well-addressed during this meeting.

Aware that plenty of attention is likely to be given to problems at this level, I want to focus at a broader scale. One major problem in trying to do this is that the life histories and migratory status of many groups— especially clupeid shads, grey mullets, and diverse eleotrids and gobies—are poorly understood. Thus some species regarded as under threat by IUCN may be diadromous without this yet being recognised. So, here is a critical issue for managing the conservation of diadromous fishes: <u>To accurately identify what species actually are</u>

diadromous and to clarify their patterns of migration. This is a significant, international biodiversity issue that takes the field of enquiry well beyond knowing what species exist, to knowing something of their ecology as a basis for conservation. With diadromous fishes, a critical aspect of conservation ecology is their migratory strategies.

The IUCN listing of the conservation status of species known or thought to be diadromous

I will start by examining the conservation status of diadromous fishes largely as revealed by the "1996 IUCN Red List of Threatened Animals" (Baillie & Groombridge 1996). This listing groups species according to their perceived conservation threat (definitions in Baillie and Groombridge 1996) but as the text does not allude to diadromy in any form, the interpretations of what species in the IUCN listing are diadromous, are mine. These are the following (diadromous migratory strategy for each species in parentheses):

Extinct:
New Zealand grayling, *Prototroctes oxyrhynchus* (New Zealand) (amphidromous)

Critically endangered:
Common sturgeon, *Acipenser sturio* (eastern Atlantic/Mediterranean, Baltic to Black Sea) (anadromous)

Endangered:
Ship sturgeon, *Acipenser nudiventris* (Aral, Black, Azov and Caspian Seas) (anadromous)
Stellate sturgeon, *Acipenser stellatus* (Caspian, Black, Azov and Aegean Seas) (anadromous)
Persian sturgeon, *Acipenser persicus* (Caspian and Black Seas) (anadromous)
Russian sturgeon, *Acipenser guldenstaedti* (Caspian, Black and Azov Seas) (anadromous)
Amur sturgeon, *Acipenser schrencki* (Amur River, western Pacific) (anadromous)
Chinese sturgeon, *Acipenser sinensis* (boreal western Pacific) (anadromous)
Kaluga, *Huso dauricus* (boreal western Pacific) (anadromous)
Beluga, *Huso huso* (Caspian, Black, Azov and Adriatic Seas) (anadromous)
Alabama shad, *Alosa alabamae* (Gulf of Mexico) (anadromous)
Delta smelt, *Hypomesus transpacificus* (Pacific coast of North America) (anadromous)

Vulnerable:
Siberian sturgeon, *Acipenser baieri* (Siberian and Arctic Russia and Baltic) (anadromous)
Shortnose sturgeon, *Acipenser brevirostrum* (western North Atlantic) (anadromous)
Green sturgeon, *Acipenser medirostris* (boreal/sub-Arctic Pacific) (anadromous)
Sterlet, *Acipenser ruthenus* (Baltic, Arctic Russia, Caspian, Black, Azov Seas) (anadromous)
Adriatic sturgeon, *Acipenser naccari* (Adriatic Sea) (anadromous)
Ariakehimeshirauo, *Neosalanx regani* (Japan) (anadromous)
Australian grayling, *Prototroctes maraena* (Australia) (amphidromous)
Giant kokopu, *Galaxias argenteus* (New Zealand) (amphidromous)
Shortjawed kokopu, *Galaxias postvectis* (New Zealand) (amphidromous)
Acadian whitefish, *Coregonus huntsmani* (western Atlantic) (anadromous)
Bull trout, *Salvelinus confluentus* (western North America) (anadromous?)
----------, *Lentipes whittenorum* (Indonesia) (amphidromous?)
----------, *Sicyopus axillimentus* (Philippines) (amphidromous?)
----------, *Stiphodon surrufus* (Philippines) (amphidromous?)

Lower risk:
River lamprey, *Lampetra fluviatilis* (eastern Atlantic/Mediterranean) (anadromous)
Atlantic sturgeon, *Acipenser oxyrhynchus* (western Atlantic) (anadromous)
White sturgeon, *Acipenser transmontanus* (eastern Pacific)
O'opu nopili, *Sicydium stimpsoni* (Hawaii) (amphidromous)

Data deficient:
------------ *Mordacia lapicida* (Chile) (anadromous)
Allis shad, *Alosa alosa* (eastern Atlantic) (anadromous)
Twaite shad, *Alosa fallax* (eastern Atlantic) (anadromous)
------------ *Clupeonella cultiventris* (Caspian Sea) (anadromous)
Smelt, *Osmerus eperlanus* (eastern Atlantic) (anadromous)
Vendace, *Coregonus albula* (eastern Atlantic) (anadromous)
-----------, *Coregonus lavaretus* (eastern Atlantic) (anadromous)
Large bottom whitefish, *Coregonus nasus* (boreal) (anadromous)
Houting, *Coregonus oxyrinchis* (eastern Atlantic) (anadromous)
----------, *Stenodus leucichthys* (boreal) (anadromous)
O'opu, *Eleotris sandwicensis* (Hawaii) (amphidromous)
O'opu nakea, *Awaous stamineus* (Hawaii) (amphidromous)
O'opu alamoo, *Lentipes concolor* (Hawaii), (amphidromous)
Redtailed goby, *Sicyopus halei* (Sri Lanka) (amphidromous?)
Lipstick goby, *Sicyopus janklaasi* (Sri Lanka) (amphidromous?)

Some of the species listed above are uncertainly diadromous, particularly the sicydiine gobies which are included on the basis that most are thought to be amphidromous (Parenti and Maciolek 1993).

A significant number of species is in the "Data deficient" category. Data deficient can mean many things, varying from:

- "There is concern, but we need to know more to be more assured of the species' conservation status, etc.", to
- "There is concern, but we don't know enough to make a preliminary assessment".

And, presumably not listed are further species about which:

- "We don't yet know enough to be concerned about what is known or to be concerned that we don't know enough to be concerned".

Again, the sicydiine gobies belong amongst such fishes, and I suspect that there are also other goby groups, as well as some of the tropical shads. Grey mullets (Mugilidae) are another problem group.

I have had real difficulty getting information about these fishes. Their taxonomies, distributions and life histories are poorly defined in many instances. In geographical terms, we are looking particularly at information deficiencies in the whole of Asia, from the Red Sea east to China, south to Indonesia and New Guinea, and also small, tropical and subtropical islands right around the globe. But, it seems to me that life histories of even some of the lesser species of the Gulf of Mexico coastal streams, such as gobies, are poorly elucidated and more may be diadromous than are presently recognised (especially given the lack of recognition of amphidromy by many North American fishery biologists (see McDowall 1997) - e.g. Nelson (1994) assigns galaxiids that I consider amphidromous to anadromy.

Also not given listing by IUCN are the races and/or stocks of northern cool-temperate salmonids that are under serious threat (Nehlsen et al. 1991; Huntington et al. 1996; Baker et al. 1996; Slaney et al. 1996). There are very few groups about which we know as much as we do about salmonids, and here, in a way, the problem may be knowing so much that the problems are almost unmanageable. In part solving this question seems to have become a question of knowing what is an evolutionarily significant population or group of populations that requires special conservation attention (Waples 1995). And it seems to me that some complex, statutory/legal questions become implicated.

I am far from sure that the IUCN listing gives a comprehensive or balanced view. Notwithstanding serious efforts by IUCN to develop rigorous, repeatable and defensible criteria for ranking species, at two ends of the spectrum there are issues that need attention. No-one can provide for the protection of species whose status and ecology are unknown or poorly known, and the international push for more attention to biodiversity is the only solution. On the other hand, intensity of effort applied to understanding the conservation status of species, and the statutory foundations for providing protection, vary widely between nations. The Australian Society for Fish Biology, for instance, has a very vigorous and continual process of evaluation and re-evaluation (Wager and Jackson 1993; Jackson 1997), and you will find a large number of species listed from Australia by IUCN (Baillie and Groombridge 1996). This may reflect high vigilance by Australian fish biologists as much as it does a comparatively high level of threatened species there.

Different forms of diadromy and conservation status

In terms of the different forms of diadromy, it is notable that no catadromous species have been listed by IUCN. Perhaps marine spawning enhances recruitment that buffers the impacts of terrestrially-based effects on catadromous species? However, there is, I know, local concern about recruitment of glass eels of the European eel (*Anguilla anguilla*—f. Anguillidae) as a result of heavy exploitation in some parts of Europe (Moriarty 1986), as well as concern about local declines of the American eel (*A. rostrata*) in some parts of eastern North America.

Otherwise it is largely anadromous and amphidromous species that are causing concern.

Viewing the IUCN list taxonomically (Table 1, 2), anadromous sturgeons are obviously in really serious peril - but not much more so than non-anadromous sturgeons (Birstein 1995; Birstein et al. 1997). Problems of their conservation seem likely to relate more closely to the demographic idiosyncrasies of being sturgeons than of being anadromous—such as slow growth rates, high age at first maturity, and heavy exploitation because they are good to eat: see Birstein (1993) for an eloquent plea for action on sturgeon conservation (note that his evaluation of the conservation status of many eastern European sturgeons seems much more alarming than that of IUCN and he writes from personal experience). However, Birstein (1993, 1995) points out that non-fishery species are also seriously threatened, so that it is not just exploitation that is critical.

The other family in trouble is Prototroctidae, with just two species (both amphidromous) - one species in New Zealand is extinct and the other in Australia is threatened. Reasons for

TABLE 1 Fish families with threatened diadromous speci[illegible]rom Baillie and Groombridge 1996).

				Threatened species										
	Species in family	Diadromous species	% diadromous	Extinct species	Critically endangered species	Endangered species	Vulnerable species	Lower risk species	Data deficient species	# in family listed	% of family listed	Diadromous species listed	% of family	% of diadromous species in family listed
Geotriidae	1	1	100.0	-	-	-	-	-	-	0	-	0	-	-
Mordaciidae	3	2	66.7	-	-	-	1(1)‡	-	-	1	33.3	1	33.3	50.0
Petromyzontidae	41	6	14.6	-	-	-	-	-	-	0	-	0	-	-
Acipenseridae	25	6	44.0	-	6(1)‡	10(8) ‡	6(4)‡	2(2)‡	-	24	96.0	16	64.0	100.0
Anguillidae	15	15	100.0	-	-	-	-	-	-	-	-	-	-	-
Clupeidae	181	32*	17.7	-	-	1(1) ‡	3(0) ‡	-	7(4)‡	11	6.1	5	2.8	15.6
Engraulidae	139	2*	1.4	-	-	-	-	-	-	-	-	-	-	-
Ariidae	120	1*	0.8	-	-	-	-	-	5(0)‡	5	4.2	0	0	0
Salmonidae	66	27	40.9	4(0)‡	4(0)‡	5(0) ‡	10(2)‡	-	14(5)‡	37	56.1	7	10.6	25.9
Osmeridae	14	7	50.0	-	-	1(1) ‡	-	-	2(1)‡	3	21.4	2	14.3	28.6
Salangidae	14	11*	78.6	-	-	-	1(1)‡	-	-	1	7.1	1	7.1	9.1
Galaxiidae	45	7	15.6	-	4(0)‡	-	9(2)‡	4(0) ‡	5(0)‡	22	48.8	2	4.4	28.6
Aplochitonidae	3	3	100.0	-	-	-	-	-	-	-	-	-	-	-
Retropinnidae	3	2	61.7	-	-	-	-	-	-		-	-	-	-
Prototroctidae	2	2	100.0	1(1)‡	-	-	1(1)‡	-	-	2	100.0	2	100.0	100.0
Gadidae	30	1	3.3	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	7	2	28.6	-	-	-	-	-	-	-	-	-	-	-
Syngnathidae	215	1	0.5	-	-	-	-	-	11(0)‡	11	5.1	0	0	0
Percichthyidae	22	4	18.2	-	-	-	-	-	5(0)‡	5	22.7	0	0	0
Lutjanidae	125	1*	0.8	-	-	-	-	-	-	-	-	-	-	-
Centropomidae	22	1*	4.5	-	-	-	-	-	-	-	-	-	-	-
Kuhliidae	8	3*	37.5	-	-	-	-	-	-	-	-	-	-	-
Terapontidae	45	1	2.2	-	-	-	-	6(0) ‡	5(0)‡	11	24.4	0	0	0
Bovichtidae	11	1	9.1	-	-	-	-	-	-	-	-	-	-	-
Pinguipedidae	50	1	2.0	-	-	-	-	-	-	-	-	-	-	-
Gobiidae	1875	45*	2.4	-	5(0)‡	-	18(4)‡	12(1) ‡	22(4)‡	57	3.0	9	0.5	20.0
Eleotridae	150	9*	6.0	-	-	-	8(0)‡	8(0) ‡	5(1)‡	21	14.0	1	0.7	11.1
Rhyacichthyidae	2	1	50.0	-	-	-	-	-	-	-	-	-	-	-
Mugilidae	80	15*	18.8	-	-(1)‡	0	-	-	-	1	1.3	0	0	0
Cottidae	115	6	5.2	1(0)‡	-	-	-	-	-	1	0.9	0	0	0
Scorpaenidae	388	1	0.3	-	-	-	-	-	-	-	-	-	-	-
Pleuronectidae	93	3*	3.2	-	-	-	-	-	-	-	-	-	-	-
Soleidae	89	1*	1.1	-	-	-	-	-	-	-	-	-	-	-
										213		40		

* number very uncertain

‡ number of diadromous species in parentheses

TABLE 2 Fish families and geographical regions with threatened species.

	Western North Atlantic	Eastern North Atlantic and Mediterranean	Boreal North Pacific	Caspian, Black, Adriatic Seas, etc.	Hawaii	Other	Total	Source of "other"in listing
Mordaciidae	-	-	-	-	-	1	1	Chile
Petromyzontidae	-	1	-	-	-	-	1	
Acipenseridae	2	3	5	6	-	-	16	
Clupeidae	1	2	-	1	-	-	4	
Salmonidae	1	3	3	-	-	-	7	
Osmeridae	-	1	1	-	-	-	2	
Salangidae	-	-	-	-	-	1	1	Japan
Galaxiidae	-	-	-	-	-	2	2	New Zealand
Prototroctidae	-	-	-	-	-	2	2	New Zealand/Australia
Gobiidae	-	-	-	-	3	5	8	Sri Lanka (2), Phillipines (2), \Indonesia
Eleotridae	-	-	-	-	1	-	1	
Total	4	10	9	7	4	11	45	

extinction and decline in this family are poorly understood. Possibly it relates to a combination of the effects of deforestation and trout introductions, but this is speculative (McDowall 1990). It is too late for the extinct New Zealand species, and we are presently at a loss to know how to reverse the process in the Australian species (but see **Sources and sinks**, below).

Viewing the list geographically (Table 2), it is clear that the most serious areas of conservation concern are eastern Europe (Caspian, Black, Azov, Aral and Adriatic Seas) and the boreal North Pacific, but this emphasis largely is generated, once again, by the dire straits of the sturgeons. Other diadromous fishes in North America and parts of Europe are also in serious trouble, and this is probably in line with high density human populations, serious estuarine habitat degradation, losses of access to critical habitats caused by impoundment, and heavy exploitation that fish populations there have been exposed to.

The serious state of the Hawaiian riverine fish fauna is an enigma. Four of Hawaii's five species of indigenous freshwater fishes (all amphidromous gobioids) are listed as under some form of threat or are data deficient (Baillie and Groombridge 1996), and concerns about their conservation have been discussed at some length (Devick et al. 1992; Fitzsimons & Nishimoto 1995). These conservation concerns are, perhaps, more surprising than for species in Europe, given lower human population densities and industrialisation in Hawaii; but they are consistent with the generally imperilled conservation status of the Hawaiian biota (Wagner & Funk 1995). High levels of impacts might be unexpected, given that there is apparently not such great pressure on the Hawaiian freshwater fish fauna from introduced predators or competitors as there is on the terrestrial fauna of these islands.

Thus, there appear to be few generalisations applicable to understanding the conservation status of diadromous fishes that are distinct from those relating either to the fact that they are migratory within river systems (like many non-diadromous fishes), or that they are subject to heavy exploitation and are impacted by habitat deterioration (like other freshwater fishes). The drying up of the Aral Sea (Birstein 1995) is the only instance I am aware of where a serious threat to any diadromous species' survival relates specifically to its marine life stages. Otherwise, there presently seems to be no evidence for conservation issues, other than possible overexploitation, during marine life stages of Pacific salmons (genus *Oncorhynchus*) in the boreal North Pacific Ocean. This is a fisheries management issue.

Differing life history strategies of diadromous fishes

There are few obvious idiosyncrasies of explicitly diadromous life histories that expose diadromous fishes to threat. The distinctive feature of diadromy, compared with migratory behaviour in other migratory fishes, is the regular, almost obligatory movement between marine and fresh waters through estuaries. Estuaries are habitats that have suffered severely as a result of human impacts, especially from frequent establishment of population centres and industries around large river mouths throughout the world. The universal need for diadromous species to pass through estuaries exposes them to the pervasive effects of estuarine habitat degradation, as well as river mouth closure in some localities. Clearly, there are instances where habitat degradation in estuaries and the lower reaches of rivers has contributed to declines of riverine stocks of species in many parts of the world, e.g. Atlantic salmon, *Salmo salar* (f. Salmonidae) in the River Thames in England, and destruction of estuarine spawning grounds of inanga, *Galaxias maculatus* (f. Galaxiidae), around the shores of many New Zealand river mouths where cities have developed. However, I am unaware that this has explicitly affected any diadromous fishes to the extent that their survival is threatened.

The migrations up stream by diadromous fishes do expose them to risks, from impoundment, dewatered river reaches, and point source polluting discharges, but these are no different from the same effects on non-diadromous (potamodromous) riverine migratory species. However, it is likely that the great distances that some diadromous species migrate are at the upper extreme of migration distances, and that they are therefore more likely to be influenced than non-diadromous species on the grounds of simple probability. There are numerous instances all over the world of harmful effects of impoundments on migratory fishes, including diadromous species.

Passage by diadromous fishes through physical bottlenecks, typically at the mouths of rivers, makes them very easy to harvest intensively and efficiently, and this exposes them to risk of decline. Undoubtedly the most extreme case of this is the Tasmanian whitebait, *Lovettia sealii* (f. Aplochitonidae) which, although not regarded as threatened, underwent a very rapid and huge decline in the late 1940s and early 1950s from which it has never recovered, despite closure of its fishery nearly 50 years ago (Fig. 2).

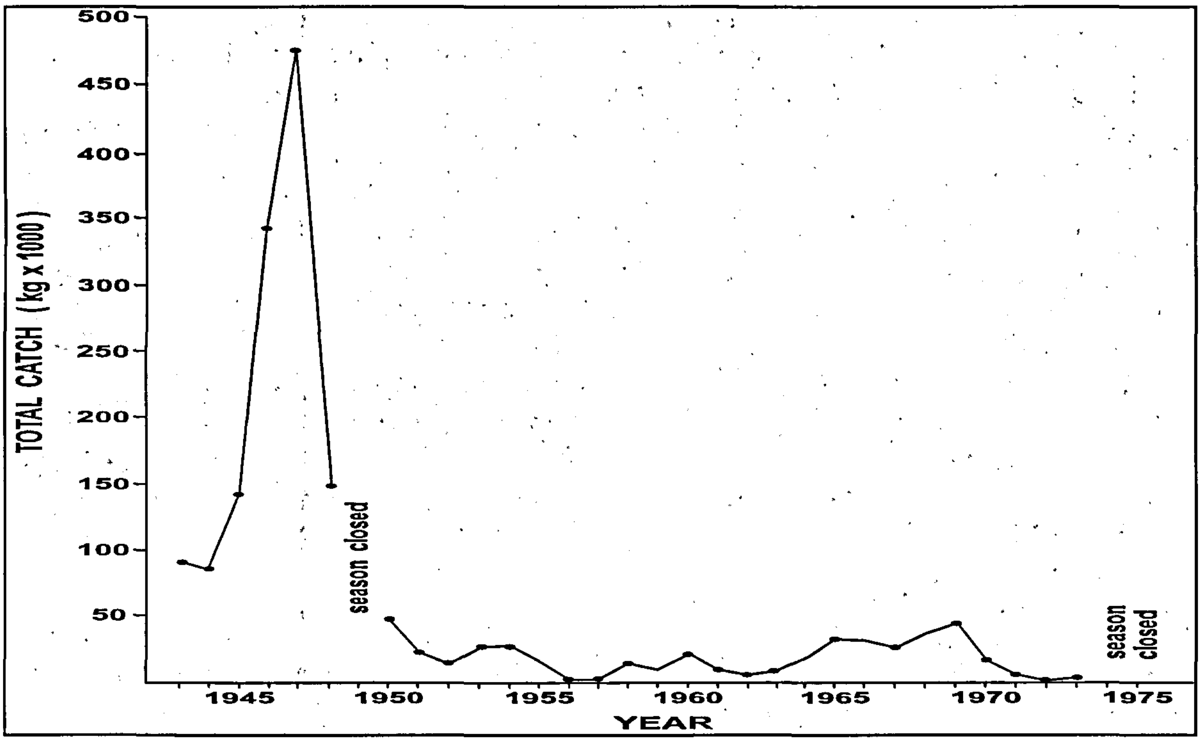

Fig. 2. Catch in the Tasmanian whitebait (*Lovettia* sealii) fishery (from Fulton 1984)

In this instance, failure of the populations to recover after closure of the fishery may point to the coincidental effects of both the beginning of intensive fishery exploitation and some other harmful habitat deterioration.

When addressing conservation and extinction issues in diadromous fishes, there is a critical need to do so in the context of the different types of migratory strategies undertaken by the wide diversity of diadromous fishes—attention to the conservation needs of diadromous fishes must be given in an explicit awareness that different forms of diadromy involve different migratory strategies and behaviours by different life stages with different migratory abilities.

When he first introduced the term diadromy in 1949, George Myers also defined three sub-categories (Myers 1949) (see Fig. 1). Two of these, anadromy and catadromy, were already old and quite widely used terms, although their usage was, and still often is, confusing and inconsistent. However, the third term, amphidromy, was new. Anadromy and catadromy continue to be widely used, but amphidromy has achieved less acceptance. This is not, in my view, due to it being a less valid term or less distinct phenomenon. Partly it is because it has been misunderstood, and partly because the distributions of amphidromous fishes tend to correlate negatively with the distribution of ichthyologists and biologists. This applies to the extent that some workers discount the term altogether, or describe it as a deviant form of anadromy (Balon & Bruton 1994). By contrast, the term is used routinely by the rather rarer biologists who work in regions, or on groups of fishes, in which amphidromy is a common phenomenon—such as fishes of Japan, Hawaii, the southwestern Pacific (Australia and New Zealand), and/or who study sicydiine gobies, eleotrids and galaxiids (Nishimoto & Kuamoo 1991; Radtke & Kinzie 1991; Parenti and Maciolek 1993; Fitzsimons & Nishimoto 1995; McDowall 1997; Pringle 1997). There is no doubt that it is a useful and heuristic term.

Although commentators have suggested that amphidromy is closest to anadromy (Balon and Bruton 1994; Gross 1987) there are also strong similarities between amphidromy and catadromy (Fig. 1). It is not my purpose here to further defend or further define amphidromy (but see McDowall 1997). What I do want to emphasise are the differences between the three forms of diadromy, in the way the fish exploit freshwater habitats, and what this means for understanding and mitigating conservation/extinction problems.

Biologists familiar with anadromy, as expressed in salmonids, osmerids, clupeids, lampreys, and other groups, typically envisage invasion of rivers from the sea by large, adult, well-matured individuals, often with their gonads well developed. Migration is largely a process of getting to the spawning grounds, often long distances upstream, as rapidly as possible to minimise mortalities and energy expenditure, and to maximise availability of energy to invest in generating reproductive products and to sustain spawning activity. This must be seen as a broad generalisation—for which there are exceptions: for example, there are some species that spend unusually long time periods during their upstream freshwater migration, such as spring migrating stocks of some autumn to winter spawning chinook salmon (Healey 1991). Moreover, the southern pouched lamprey (*Geotria australis*, f. Geotriidae), spends so long between migrating from the sea and reaching sexual maturity (about 14-16 months - Potter et al. 1980; Glova 1995) that there are actually two breeding cohorts at different stages of maturation (a year apart) simultaneously in river systems where it spawns. But even though present in rivers for long to short periods, the upstream-migrating anadromous spawners are essentially passive members of the freshwater ecosystems that they enter for maturation, until they do eventually spawn.

In general, the spawning sites of anadromous species represent the species' upstream limits in river systems. After the young hatch there develops a trajectory of downstream movement of feeding and growing juveniles that, over periods of a few weeks, to months, or even years, find their way to sea. There are some stocks of sockeye salmon (*Oncorhynchus nerka*) in which there is an upstream migration from the spawning grounds into lakes (Burgner 1991), but these are exceptional. Depending on how rapidly the progeny of anadromous species make their way to sea, their presence in rivers may be highly variable seasonally, e.g. the young of pink and chum salmon, *Oncorhynchus gorbuscha* and *O. keta*, are present in fresh water for only days or weeks in the early to mid spring (Heard 1991; Salo 1991); in other Pacific salmons this phase may last several weeks to months over the spring and summer, but again there are very strong seasonal modes in abundance and distribution (Burgner 1991; Healey 1991; Sandercock 1991). Alosid shads may also spend several months in fresh water after hatching and before departing for the sea (reviewed in McDowall 1988). However, the newly hatched larvae of many anadromous species go straight to sea, as in Osmeridae, Salangidae, the Australian aplochitonid *Lovettia sealii*, and New Zealand Retropinnidae (see McDowall 1988)

The processes of entry into fresh water, and growth and maturation there by amphidromous and catadromous species are very different from those in anadromous species. In both amphidromous and catadromous species, entry to rivers takes place as small to well-grown juveniles, varying from about 15 to 75 mm in length, the upper extreme being anguillid glass eels which are very slender, and so of very small mass. Migrating juveniles of most species are less than 50 mm long and many less than 30 mm. Thus both catadromous and amphidromous species at entry to fresh water are very small and quite different from anadromous species at migration.

At least in New Zealand's amphidromous species, what happens is that the small immigrant juveniles settle in the lower reaches of rivers, and over a period of months or even years gradually make their way upstream into habitats suitable for feeding, growth, and maturation. Distribution patterns for these species are thus anchored in the lower reaches of river systems and because the species are in almost all instances able to find suitable habitats no great distance upstream, there is declining frequency of occurrence and abundance with both increasing elevation and distance up stream. Fig 3 shows patterns of distribution for 12 mostly amphidromous and catadromous species in rivers of the West Coast of the South Island of New Zealand; the figure plots the percentage frequency of occurrence of each species across intervals at 10m intervals of elevation, and so adjusts for differences in sampling intensity at different elevations. In almost all species there is a greatest concentration at downstream locations, highly varying inland penetration, but almost always declining frequency of occurrence. There is no hint of diadromous species having primarily inland ranges.

There is also evidence for changing age and size structure of the populations of amphidromous with distance. Lower down in river systems all age classes are present, but because upstream penetration takes time, the fish are older/larger by the time they get further up stream, and this is reflected in a changing size and age distributions (Fig. 4). There are thus downstream-upstream trajectories of declining occurrence/abundance, and increasing mean

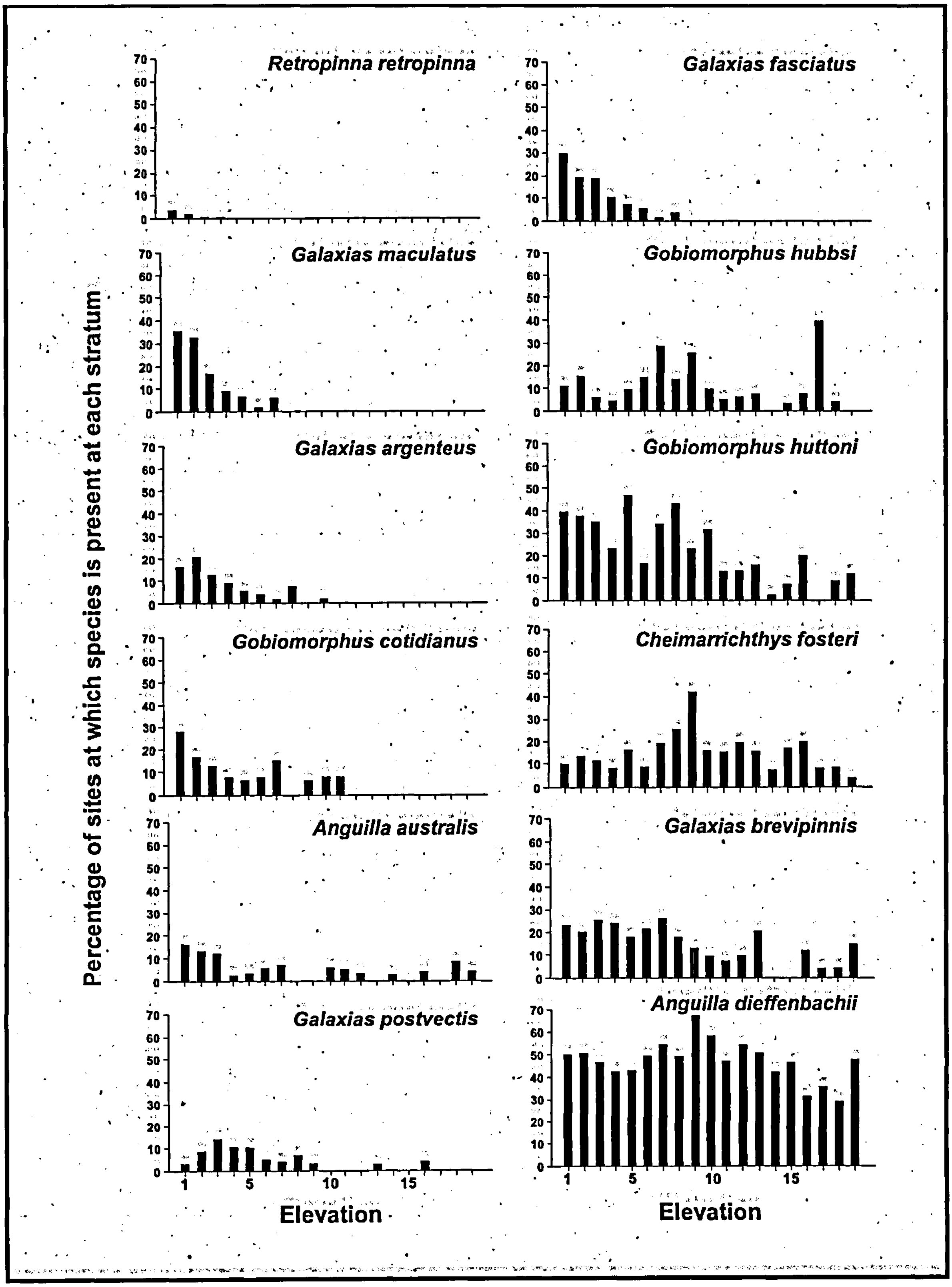

Fig. 3. Occurrence of diadromous fishes in West Coast, South Island, New Zealand rivers presented as 25 m elevation strata to standardise occurrence against varied sampling intensity at different elevations.

and modal age and size. The process of entry into rivers and occupation of riverine habitats is perhaps best described as insinuation. Understanding these strategies of invasion is crucial to interpreting amphidromous and catadromous species' conservation needs.

Species differ in several parameters related to their invasion of river systems—in their swimming strength, climbing ability, and instinctive migratory drive. These differences result in species-characteristic patterns of occurrence. Those that are weak migrators, as a result of either or both of weak swimming ability and low upstream migratory drive occur only at low elevations and distances from the sea. As one or both of ability and drive increase, so the distribution spreads inland, but these species remain present at low elevations and distances inland—thus they just become more widespread. None of New Zealand's amphidromous species is absent at low elevations distances and present only further inland (Fig. 3). These patterns do not apply to all amphidromous species, e.g. the Hawaiian *Lentipes concolor* (f. Gobiidae—a species listed as data deficient by IUCN) has a distribution that is primarily well inland and at high elevations and, apart from upstream migratory juvenile stages, is not found at low elevations (Devick et al. 1992). It's pattern of distribution within Hawaiian river systems more closely resembles that of an anadromous species.

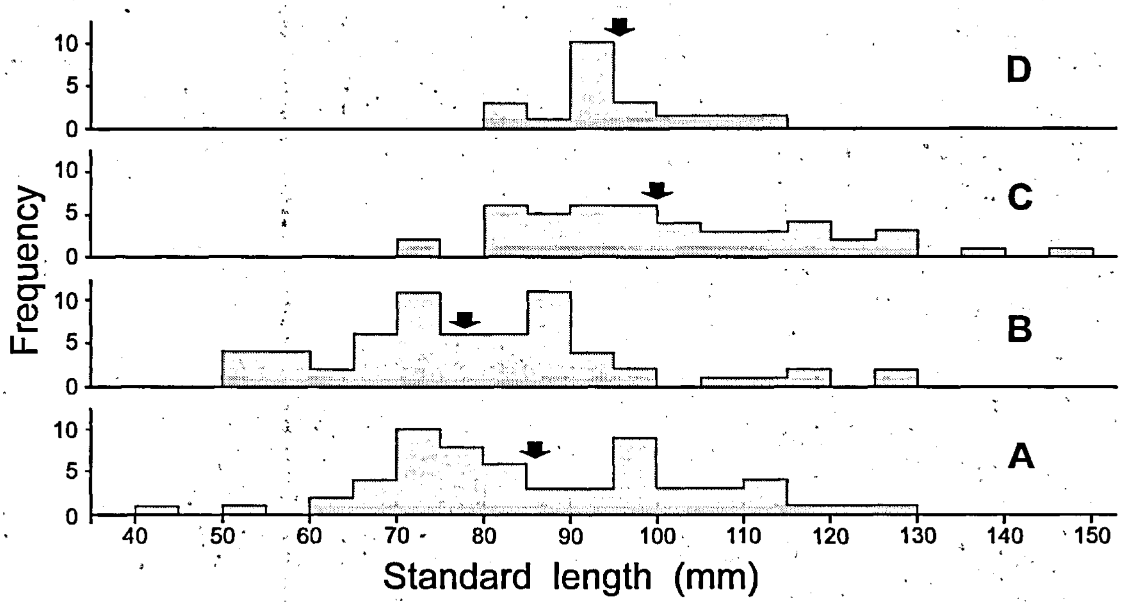

Fig. 4. size/frequency distribution of populations of torrentfish, *Cheimarrichthys fosteri* at different distances up stream from the sea in the Waikanae River, New Zealand (A. 2.8 km up stream; B. 5.6 km; C. 10.6 km; D. 12 km)

However, the chief point that I want to make is that the rapid upstream movement by large, highly mobile, adult, anadromous fishes is not the only migratory pattern that needs consideration when reviewing conservation problems in diadromous fishes.

We need also to take account of the way small upstream-moving juveniles of amphidromous and catadromous species migrate. Their ability to penetrate inland is based on quite distinctive swimming skills. Typically, they are climbers, especially those that move well inland, and many of them are capable of getting past some formidable barriers. The champion is perhaps *Lentipes concolor*, which Devick et al. (1992) reported above individual waterfalls more than 140 m high and above a cumulative height of sequential falls exceeding 600 m. However, this species is not alone in its climbing ability; other gobies, anguillid eels and some galaxiids are not far behind. Without anything more than a damp, exposed concrete dam-face, elvers get over dams in New Zealand over 40 m high. I have found juvenile galaxiids above falls that I estimate as 60 m high.

Because of the different modes of upstream penetration, the technology of fish passes for amphidromous and catadromous has, also, to be different. The very strongly developed fish pass technology for salmonids and other larger jumpers is often based on resting pools and carefully designed low-height barriers that fish can jump. These are of little or no use to amphidromous and catadromous fishes, and may be total barriers for them. They need fish passes that facilitate climbing in contact with a substrate in the absence of powerful flushing/turbulent flows. Provided with a suitable fish pass, there is virtually no height that these amazing little fish cannot get past; they will seemingly keep on going until they run out of energy. The beauty of this approach is that appropriate fish passes are cheap, simple, easy to install after a dam has been built, and require minimal water flows. When elvers and juvenile galaxiids were provided with a fish pass comprising a large bottle-brush-type insert in a plastic pipe, they streamed up a 75 m high New Zealand dam in such numbers that deoxygenation and waste excretions by fish well up the fish pass suffocated those lower down.

To deal with these fish, first there is a need to recognise that they exist, and second to establish a distinctive mind-set that accommodates their specific migratory behaviours and abilities.

Sources and sinks

Homing of spawning anadromous fishes back to natal streams is a core idea in the ecology and behaviour of anadromous fishes, particularly in salmonids, though it is also raised for other anadromous taxa (Jessop 1994; Dittman and Quinn 1996). However, I know of no serious discussion of the likelihood of homing in other forms of diadromous migrations. In fact it is impossible in catadromous fishes since the natal spawning area is at sea; juvenile catadromous fishes are thus entering rivers from which spawning adults have formerly departed. Amongst amphidromous fishes, emigration from rivers is as newly hatched larvae, and the prospect that they can return to natal rivers on the basis of memorised natal river characteristics seems somewhat far-fetched.

The concept of populations in highly productive habitats ("sources") providing for recruitment into unproductive habitats ("sinks") has recently been emphasised (Pulliam 1988; Dunning et al. 1992) as a potentially important process for understanding community and landscape ecology. A mechanism of this sort was suggested as an explanation for the extinction of the New Zealand grayling (McDowall 1978, 1990), and has potentially useful application to diadromous fishes. The process has the potential to set a species on a trajectory to extinction if the drain on the source populations by the sink populations is sufficiently severe—especially if the productivity of recruits in source populations is erratic and/or habitats of source populations are under threat of degradation. In the case of the southern graylings, possibly the continuous drain on source populations may have been more than can be sustained.

Furthermore, Hildrew (1996) has pointed out that the conservation status of a species or community can only be evaluated properly if the balance between sources and sinks is understood. In fact the widespread distribution and local abundance of a species, that is interpreted as favourable, may even disadvantage a diadromous species and contribute to its decline.

The concept of sources and sinks in relation to diadromous fish migrations may seem counterintuitive in evolutionary/selective terms. However, diadromous fishes entering rivers are probably responding to environmental signals that guide them into specific rivers, signals that correlate with the suitability of the upstream habitats - probably the geology, soils and vegetation through which the water flowing down stream passes and obtains its "character". These signals may increasingly be misleading as a result of human modification of catchments if the critical signals remain present but the habitat up stream is degraded. Impoundments of river systems would be a classic example.

The question of landlocked stocks

It is well known that in many diadromous species, landlocked or freshwater-limited populations develop, most often in lakes. This life history flexibility provides an opportunity to provide protection for populations by limiting their passage needs and avoiding them having to pass through polluted waters or places where exploitation is heavy. However, it is really important to recognise that a landlocked population of a diadromous species represents a seriously reduced form of the species, certainly behaviourally and probably genetically. Attempts to provide for the conservation needs of a species though protection of landlocked stocks should therefore be strenuously resisted, unless this is a last opportunity to ensure a species survival (McDowall 1992).

Conclusions

1. Probably the most critical issue for conservation of diadromous fishes is to learn which species are diadromous and to understand their migration strategies;
2. Some diadromous fishes are in serious conservation peril, particularly Acipenseridae and Prototroctidae;
3. There is nothing specific about their being diadromous that contributes significantly to that peril that is not also true of similar species that are migratory in fresh water;
4. There is real concern about the condition and habitat/water quality in the lower reaches or rivers in many parts of the world;
5. Two distinct patterns of penetration of river systems must be given careful consideration when attending to the migratory needs of diadromous fishes:

- The rapid penetration of large, strong-swimming, adult anadromous fishes, many of which can leap substantial barriers, and
- The slow penetration by small fishes that move along or even within the substrate, and which can overcome incredible barriers by climbing, as long as some simple consideration is given to their needs.

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