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Biology and conservation of sturgeon and paddlefish

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Contents

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Abstract

The Acipenseriformes (sturgeon and paddlefish) live in the Northern Hemisphere; half of these species live in Europe, mostly in the Ponto-Caspian region, one third in North America, and the rest in East Asia and Siberia. They reproduce in freshwater and most of them migrate to the sea, either living in brackish water (Caspian, Azov, Black and Baltic Seas) or in full seawater on the oceanic continental shelf. Most species feed on benthic organisms. Puberty usually occurs late in life (5–30 years of age) and adult males and females do not spawn on an annual basis. Adults continue to grow and some species such as the beluga (*Huso huso*) have reached 100 years of age and more than 1,000 kg weight. Stocks of sturgeons are dramatically decreasing, particularly in Eurasia; the world sturgeon catch was nearly 28,000 t in 1982 and less than 2,000 t by 1999. This decline resulted from overfishing and environmental degradation such as: accumulation of pollutants in sediments, damming of rivers, and restricting water flows, which become unfavorable to migration and reproduction. Several protective measures have been instituted; for example, fishing regulation, habitat restoration, juvenile stocking, and the CITES listing of all sturgeon products including caviar. In addition, sturgeon farming presently yields more than 2,000 t per year (equivalent to wild sturgeon landings) and about 15 t of caviar. Hopefully, this artificial production will contribute to a reduction of fishing pressure and lead to the rehabilitation of wild stocks.

Introduction

Some knowledge of the sturgeons was available by the end of the 19th century. In Russia, the first artificial reproduction of sturgeon occurred in 1869 (Milshteyn, 1969). Ryder (1890) described techniques of artificial reproduction and caviar processing in North America. Research continued in the early 20th century with major contributions in the areas of biology and systematics: Russia (Berg (1948) and his successors (Holcik, 1989)), Romania (Antipa 1933), France (Magnin, 1962) and North America (Vladykov, 1955). Recently, new interest has been focused on the Acipenseriformes (sturgeon and Polyodontidae) resulting in the development of research programs and international conferences; Bordeaux 1990 (Williot, 1991), Moscow 1993 (Ghershanovich and Smith, 1995), New York 1994 (Birstein et al., 1997a), Piacenza 1997 (Rosenthal et al., 1999) and Oshkosh, Wisconsin 2001. In addition, reviews have been published on systematics, biology, farming and conservation of sturgeons (Doroshov (1985), Rochard et al. (1990, 1991), Dettlaff et al. (1993), Billard (1996/97), Ronyai and Varadi (1995), Birstein (1997)).

There is increased demand for new information about the biogeography, physiology, life history and evolutionary history of these species because most Acipenseriformes are considered endangered. This review covers these topics, particularly as they relate to useful measures of conservation and the development of sturgeon farming techniques.

Biogeography and life history

Acipenseriformes live exclusively in the Northern Hemisphere (Figure 1) and reproduce in freshwater. They migrate mostly for reproduction and feeding. Some species spend their whole lives in freshwater (e.g., sterlet (*Acipenser ruthenus*) and Siberian sturgeon (*A. baerii*)). Others migrate between freshwater and saltwater (diadromous species). Some species migrate into full seawater after they reach a certain size, generally staying on the continental shelf (e.g., European sturgeon (*A. sturio*), Atlantic sturgeon (*A. oxyrinchus*), and white sturgeon (*A. transmontanus*)). Some species migrate into brackish water in the Black, Azov and Caspian Seas (e.g., Russian sturgeon (*A. gueldenstaedtii*), stellate sturgeon (*A. stellatus*), and beluga (*Huso huso*) (Table 1). During the growth period in sea or brackish water, many species undertake short migration into freshwater. However, somatic growth in freshwater is less than in seawater; while in freshwater, stomachs of diadromous sturgeon are often empty. Carr et al. (1996) observed that the body weight of *A. oxyrinchus de sotoi* in the Gulf of Mexico increases annually by 20% in the sea and decreases by 12% while in freshwater.

Some populations living in seawater or brackish water may adapt to accomplish the entire reproductive cycle in freshwater as illustrated by the landlocked Kootenai population of *A. transmontanus*, which was isolated above the Columbia River by a landslide 10,000 years BP (Duke et al., 1999). Also, most of the Ponto-Caspian species were shown to mature in freshwater ponds in captivity. The Black, Azov and Caspian Seas were freshwater lakes 22,000–10,000 year BP (Degens and Ross, 1972) and all Pont-Euxine sturgeons currently live primarily in freshwater. Bemis and Kynard (1997) recognized 3 main patterns of migration: potamodromy (migration within a river/lake system; e.g., Scaphirhynchini, sterlet, paddlefish (*Polyodon spathula*)); anadromy (spawning occurs in freshwater but most of the life is spent at sea, e.g., most *Acipenser* and *Huso*); and freshwater amphidromy (spawning in freshwater, feeding and growth occur during migration into salt water, e.g., shortnose sturgeon (*A. brevirostrum*)). The same authors observed that, when two species are present in marine coastal rivers, one is anadromous and the other potadromous.

Bemis and Kynard (1997) based a biogeographic analysis of the living Acipenseriformes on the 85 rivers in which spawning occurs and identified nine biogeographical provinces with quite different numbers of species: North Eastern Pacific (2), Great Lakes (2), North Western Atlantic (2), Mississippi-Gulf of Mexico (5), North Eastern Atlantic (2), Ponto-Caspian and other local seas (11), Siberian and Arctic Ocean (2), Amur River Basin (3), Chinese, Japanese and Okhotsk Seas (2). Although, the possibility of exchanges between provinces is limited, the same species may be found in different places; *A. ruthenus* is present in three provinces, *A. fulvescens* and *A. sturio* in two. The richness of the Ponto-Caspian province may be the result of the instability of these regions over the last 150 million years. Bemis and Kynard (1997) pointed out the presence of Scaphirynchine sturgeons in both the Ponto-Caspian and the Mississippi regions and Polyodontidae in China and the Mississippi regions; these probably

Table 1. List of extant species of the Acipenseriformes (in order of their threatened status from most to least) *A.: Acipenser*, *H.: Huso*, *P.: Pseudoscaphirhynchus*, *S.: Scaphirhynchus*

Species	English name	Ref. (1)	Historical geographic distribution	Length maxi (m)	Weight maxi (kg)	Environment (2)	Status (3)	Stocking (4)
P. fedtschenkoi (Kessler, 1872)	Syr Dar Shovelnose		Syr-Darya	0.3		fb	CR	
P. hermanni (Kessler, 1877)	Small Amu Dar Shovel.		Aral, Amu-Darya	0.3		fb	CR	
Psephurus gladius (Martens, 1862)	Chinese Paddlefish		Yangtze	3.0	300	fb ?	CR	
S. suttkusi (Williams and Clemmer, 1991)	Alabama		Alabama, Mississippi	0.8	2	f	CR	
A. dabryanus (Duméril, 1868)	Yangtze / Dabry's		China, Yangtze, Korea		750	f	CR	
A. sturio (Linnaeus, 1758)	European / Atlantic	120	Europe (North Africa)	5.0	500	s	CR	(+)
H. dauricus (Georgi, 1775)	Kaluga		Amur Riv., Japan	5.6	1000	fs	EN	
H. huso (Linnaeus, 1758)	Beluga / Giant	140	Black, Caspian Azov, Adriatic Seas	8.5	1300	b	EN	+++
P. kaufmanni (Bogdanov, 1874)	Large Amu Dar Shov.		Aral, Amu-Darya	0.4	3	fb	EN	
S. albus (Forbes and Richardson, 1905)	Pallid		Mississippi, Missouri	1.8	3	f	EN	
A. nudiventris (Lovetzky, 1828)	Ship	65	Caspian, Black and Azov Seas (Aral)	2.0	127	b	EN/CR	+++
A. sinensis (Gray, 1834)	Chinese		Yangtze, Pearl Riv., Korea, Japan	>2.0	550	s	EN	
A. schrenckii (Brandt, 1869)	Amur River		Amur River, Okhotsk and Japan Seas	2.9	200	f	EN	+
A. mikadoi (Hilgendorf, 1892)	Sakhalin		N.W. Pacific	2.0		s	EN	
A. gueldenstaedtii (Brandt, 1833)	Russian	240	Caspian, Black and Azov Seas	2.3	100	b	EN	+++
A. stellatus (Pallas, 1771)	Sevruga / Stellate	180	Black, Caspian Azov Seas	2.2	80	b	EN	+++
A. persicus (Borodin, 1897)	Persian	70	Caspian and Black Seas	2.4	70	b	EN	++
Polyodon spathula (Walbaum, 1792)	N. American Paddlefish		Mississippi Basin	2.5	100	f	VU	+
S. platorynchus (Rafinesque, 1820)	Shovelnose		Mississippi, Missouri	0.9	3	f	VU	
A. brevirostrum (Lesueur, 1818)	Shortnose		From Florida to New-Brunswick	1.4	24	f(s)	VU	+
A. fulvescens (Rafinesque, 1817)	Lake		Great Lakes and lakes of S. Canada	2.4	140	f(b)	VU	+
A. medirostris (Ayres, 1854)	Green		N. Pacific	2.1	160	s	VU	
A. ruthenus (Linnaeus, 1758)	Sterlet	130	Europe, ex. USSR Caspian, Black, Azov	1.1	16	fb	VU	+
A. baerii (Brandt, 1869)	Siberian	100	Siberia, Arctic	3.0	200	fb	VU	++
A. naccarii (Bonaparte, 1836)	Adriatic	29	Adriatic, Pô, Adige, Mediterr.			bs	VU	(+)
A. oxyrinchus (Mitchill, 1814)	Atlantic Aoo / Gulf Aod		Gulf of Mexico, Hamilton/Fundy	4.3	368	s	VU:LR	(+)
A. transmontanus (Richardson, 1836)	White		N.E. Pacific	6.1	816	s (f)(5)	LR	+

(1) Number of references quoted for European species in Holcik (1989).
(2) f: live entirely in freshwater, fb: mostly freshwater with short migration in brackish water; b: growth in brackish water; s: growth in sea water.
(3) CR: critically endangered, VU: vulnerable; EN: endangered; LR: Low risk (cf. Lelek, 1987; Johnson, 1987; Birstein et al., 1997c).
(4) stocking juveniles: +++, ++ stocking intensity in Russia; + small scale stocking; (+) experimental.
(5) one landlocked population.

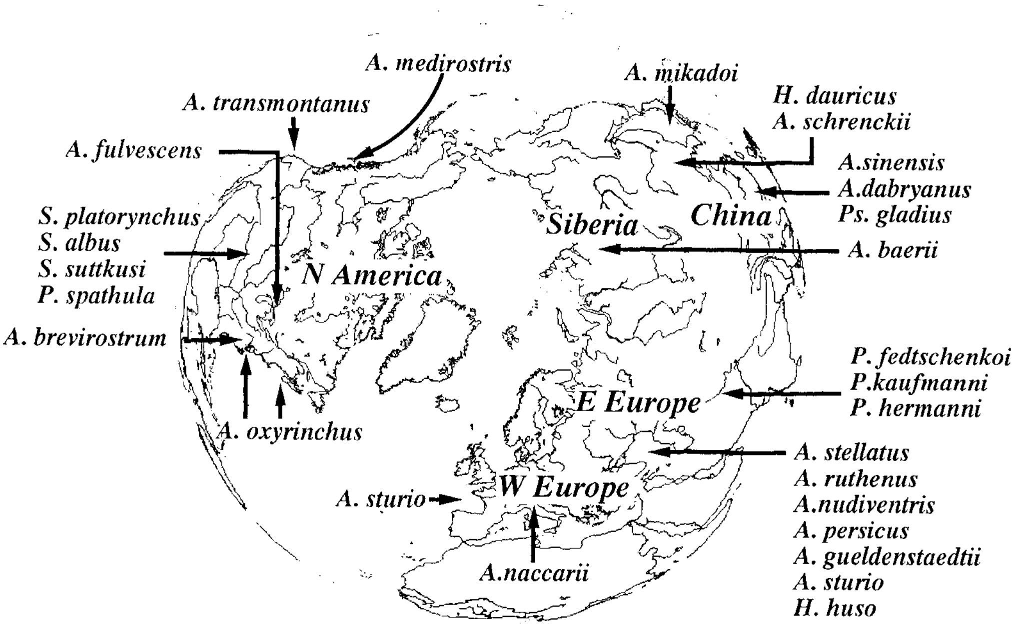

Figure 1. Geographic distribution of the Acipenseriformes.

Table 2. Age, weight and total length at puberty, average time (years) between two spawnings and longevity in the wild for several species of *Acipenser* (*A*), *Huso* (*H*), and *Pseudoscaphirhynchus* (*P*) and one farmed stock of *A. baerii*

Species	River	Age and size at puberty						Years between two spawnings		Longevity (years)	
		Years		Total length (cm)		kg					
		Male	Female	Male	Female	Male	Female	Male	Female	Historic	Present
A. sturio	Gironde	7–15	16–20	145	165	20	30			48	
H. dauricus	Amur	14–21	17–23		230			3–4	4–5		55
H. huso	Volga	14–16	19–22	160	200	30	60	3–4	5–6	107–118	60
P. kaufmanni	Amu-Darya	5–7	6–8								
A. nudiventris	Kura	6–9	12–14	100–130	140–150	10	30		2–3		
A. sinensis	Yangtze	9–17	14–26			40	120				
A. brevirostrum	Georgia	2–3	4–6	46–50	46–50				2–4		67
A. fulvescens	St. Lawrence	15–17	20–24	85–95	90–120	4–5	4–9	2–3	4–6	152	40
A. gueldenstaedtii	Volga/Danube	11–13	12–16	100	120	3	9	2–3	5	≥50	38
A. stellatus	Volga	7	9	105	120	3–4	9–10		3–4	41	30
A. ruthenus	Danube	3–5	4–7	35	40–45			1	1–2	26	22
A. persicus	Volga, Ural	15	18	122	162	12	19	2–4	2–4	38	
A. baerii	Ob, Yenissei	11–13	17–18	75–80	85–90			1-4	3-6	60	
	Farms	3–4	7–8					1–3	2–4		
A. oxyrinchus	St. Lawrence	22–24	27–28	165	190			1–5	3–5	60	
A. transmontanus	Colombia	12	16–35	120	150			3	2–11		104

Data mostly from Tsepkin and Sokolov (1971); Holcik (1989); and Rochard et al. (1991).

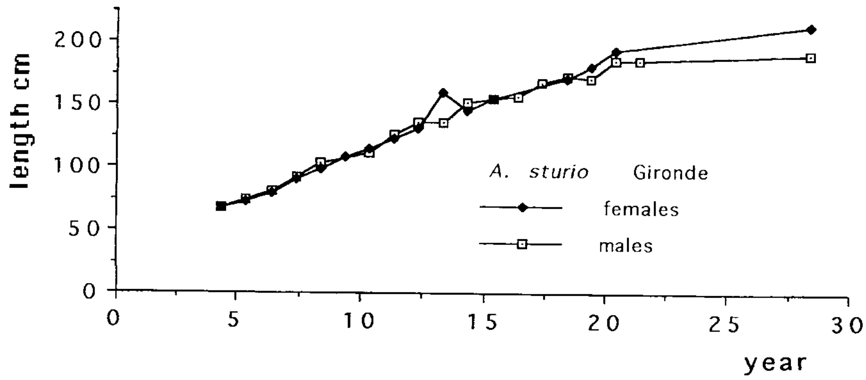

Figure 2. Growth curve in weight and total length of *Acipenser sturio* from La Gironde France; after Magnin 1962. The number of fish per year class is in the range of 5 to 30 except after 30 years (only 1 or 2 individuals were available). Puberty occurs at about 15 years.

support an old link as Scaphirynchini and Polyodontidae were present in North America in the Late Cretaceous. Five anadromous Acipenser species, found in the three Pacific provinces, appear to form a monophyletic group; another species from these regions, *A. dabryanus*, lies outside this group but stays in freshwater and is restricted to the Yangtze. Several species, such as *A. baerii*, *A. fulvescens*, and *A. oxyrinchus*, were impacted by Pleistocene glaciations and probably occupied some unique refugium.

The life cycle of Acipenseriformes is generally quite long with puberty occurring late in life (Table 2). Some species (e.g., beluga) can live for 100 years and exceed 1,000 kg in mass (Table 1). Such specimens are no longer found but fish over 100 kg are still caught. Sturgeon growth is continuous with age (Figure 2) and does not seem to be greatly reduced after first reproduction (see growth curves in Bain, 1997; Korkosh and Pronenko, 1998; Bruch, 1999). It is hypothesized that somatic growth is the priority for large sturgeon rather than reproduction, which does not occur every year (Table 2); thus, they reach a large size and can occupy the central part of large rivers.

Most sturgeon species feed benthically. They are dependent on the quantity and the quality of prey available. Some large-sized species (beluga or kaluga (*Huso dauricus*) of more than 40 cm in length) feed on benthic and pelagic fish and depend indirectly on the richness of both plankton and benthos (Polyaninova et al., 1999). Sturgeons possess tactile barbels located at the front of a thick-lipped, "protactile" mouth. Sturgeons also dig with their rostrum in search of food. Their eyes are very small relative to fish size and probably do not contribute much to the location and capture of prey.

Mature Acipenseriformes do not reproduce annually. Spawning rates are once in 2–11 years for females, and 1-6 years for males (Table 2). Under farm conditions, Williot and Brun (1998) showed that only 25% of *A. baerii* females reproduced annually, whereas in other situations reproduction was either biannual (54%) or triannual (11%). Reproductive effort per cycle is important, as shown by the gonado-somatic index (GSI), which reaches 3–9% in males and 10–25% in females (Table 3). Fecundity, expressed by the number of ovarian follicles prior to ovulation, depends on the size of eggs, for instance, 6,000–7,000 per kg of female body weight (diameter 3.4 × 3.8 mm) in *H. huso* and 30,000 (2.5 mm) in *A. ruthenus* (Holcik, 1989). Occasionally, fecundity is stated as number of ovulated oocytes, for instance 7,200 ova of 3.5 mm in *A. transmontanus* (Doroshov et al., 1997). Most species spawn in the spring to early summer over a large range of temperatures (6° to 25 °C, Table 4). For several diadromous Caspian sturgeon species, vernal and winter races were recognized (Berg, 1934, quoted by Pickford, 1955). Winter fish spend the winter in the river or the river mouth, hibernating in holes and eating very little or nothing. They spawn far upstream year(s) after entering the river. The vernal races do not hibernate. They enter the river on rising temperatures. Vernal fish mature in the lower river the same year. Puberty is reached earlier (they are smaller on average than winter fish) and they spawn later in the season. Gerbilskii (1951) made further distinctions between early or late vernal and autumnal migrations. Migration also depends on the flow regime of the rivers. Damming and reduction of flow rate due to agriculture irrigation in the Kuban River in the early 1980s resulted in total suppression of

Table 3. Gonad size as percentage of body weight (GSI), fecundity in thousands of eggs per kg body weight and egg size

Species	River	GSI %		Fecundity	Size of ova	
		male	female	eggs/kg ×1000	mm	mg
Acipenser sturio	Gironde		13.0-30.0	18.0-23.0	2.4–2.8	
Huso dauricus	Yangtze		14.0	3.2–15	2.5–3.5	
Huso huso	Volga	3.0–9.0	13.0–17.0	3.3	3.3-4.0	29.5
A. nudiventris	Kura, Aral Sea		11.0–23.0	9.1–21.7	1.5–3.0	12.0–15.0
A. sinensis	Yangtze				3.7–4.9	
A. gueldenstaedtii	Volga, Ural	3.9–5.5	15.0	10.8–14.8	2.8×3.2*	20.6–22.1
A. stellatus	Volga	5.8	25.9		2.0–3.0	8.0–9.0
A. persicus	Kura, Volga, Ural	6.5	20.9		3.2–3.8	
Polyodon spathula	Mississippi			9.1–2.6	2.0–3.1	3.7
A. brevirostrum	Hudson				3.0–3.2	
A. fulvescens	St. Lawrence				2.7–3.5	
A. medirostris	Sacramento, Rogue	5.7		3.0–6.0	3.2–3.7	
A. ruthenus	Danube				1.8×2–2.8×2.9*	
A. baerii	Ob, Lenisei, Lena	3.9–9.1	24.0	13.6–16.5	2.4–4.9	10.8–25.0
A. naccarii	Pô				2.0–2.4	
A. oxyrinchus	St. Lawrence		25	16	2.1–3.0	
A. transmontanus	Columbia, Fraser				3.5–4.0	

*ovoid eggs.

the anadromous autumn run of *A. stellatus* and delayed the stages of gonad maturation in females migrating in spring. All females were at stage IV final in 1999–2000 while in 1980, 40% of them were at stage III–IV (Chebanov and Savelyeva, 1999).

Sturgeon spawn in the mainstream or margins of the river on hard substrates on the bottom. The depth of the spawning place varies from a few meters to 26 m and the current velocity ranges from 0.5 to 2.2 m s^{-1} in the water column, allowing a wide dispersal of fertilized eggs (Table 4). Considering the short duration of sperm motility 1–2 min (Billard et al., 1999) good synchrony in the release of the gametes by the male and the female is likely. However, the ova remain fertile after release into freshwater for up to one hour (Dettlaff et al., 1993) so that stray eggs may be fertilized by freshly ejaculated sperm. Likewise, sperm is rapidly diluted by the high velocity of the river current. Fertilization success in sturgeon and paddlefish is increased by the presence of several micropyles in eggs (Dettlaff et al., 1993; Linhart and Kudo, 1997). According to Dettlaff and Ginsburg (1963), calcium ions are required for sperm acrosome reaction. Sulak and Clugston (1999) found that spawning waters require an appropriate amount of Ca^{++} and that abnormally high levels may induce a precocious acrosome reaction thus preventing fertilization. For many species, the environmental factors triggering spawning such as temperature, flow rate, velocity of current, appropriate spawning substrate, and the role of pheromones in sturgeon reproductive behavior remain unknown.

A. transmontanus' eggs are adhesive and are found immediately downstream of the spawning bed, attached to 3–10 cm (sometimes up to 25 cm) blocs or pebbles (Parsley et al., 1993). Water velocities of 0.5–1.5 m s^{-1} have been reported during embryogenesis (Jatteau, 1998). Depending on the species and the temperature, hatching occurs after 200–250 hours. The size of hatched larvae ranges from 6–15 mm total length. The yolk sac larvae of several species (*A. baerii, A. brevirostrum, A. stellatus*) are pelagic for 2–3 days (7–8 days for *H. huso*) and are transported downstream by currents at a velocity of up to 45 cm s^{-1} i.e., 40 km day^{-1}. After displacement from the spawning ground the yolk sac larvae settle down, usually in a much lower water velocity (1 to 5 cm s^{-1}) on coarse substrate. They start feeding on both planktonic and benthic organisms. In some species (*A. fulvescens, A. medirostris*) the yolk sac larvae remain at the bottom for few weeks before moving downstream.

After yolk absorption the larvae actively feed on benthic organisms and are usually found on homogenous sand substrate in places with water velocities < 10 cm s^{-1} (review by Jatteau, 1998). The water velocity and substrate requirements for eggs and larvae are different for fertilization, embryogenesis,

Table 4. Spawning environment of some sturgeon species
A.: Acipenser, *H.: Huso*, *P.: Pseudoscaphirhynchus*, *S.: Scaphirhynchus*
Data taken mostly from Holcik (1989), Birstein et al. (1997a), Rochard et al. (1991) and Chapman et al. (1996)

Species	Spawning time	Temperature °C	Location of spawning beds	Spawning substrate	Depth m	Current velocity m s^{-1}
Psephurus gladius	Late March–April	18.3–20		sand, gravel, cobble	10.0	0.7–0.2
A. sturio	March–Aug	7.7–22	middle reaches deep pools	gravel, stones	>5.0	1.5–2
H. dauricus	May-June	12.0–21	main river bed large side channel	pebbles	2.0–3	calm waters
H. huso	Spring	6.0–21 opti: 9–17	upper reaches higher water	stones, pebbles, gravel	4.0–15	1.5–2
P. kaufmanni	March–early May	14–16	rocky bottom		1.0–2	
A. nudiventris	April–June	15.0–25	middle reaches	gravel, pebbles,	4.0–15	1.0–2
A. sinensis	Oct–Nov	15.0–20	middle reaches of rivers	course gravel ⌀ 3–10 cm	8.0–26	0.8–1.4
A. schrenkii	May–late June		main river channel		7.0–11	0.5–2
A. gueldenstaedtii	May–June	8.0–15	main stream	gravel	4.0-25	1.0–1.5
A. stellatus	May–Sept	12.0–24 Volga 15.0–29 Kura	lower reaches by the banks	gravel rocks	2.0–14	bottom: 0.7–1.8 surface: 1.1–1.9
S. platorynchus	April–July	17.0–21	rock structure, borders of main channel, below dams	rocks, channel		
A. brevirostrum	Feb–May	Sep-15	main river channel	gravel, rubble	1.2–10.4	0.4–1.8
A. fulvescens	May–June	13.0–18	upper reaches	gravel	<3.5	below rapids & falls
A. medirostris	Spring	9.0–17	upper reaches	bedrock		below rapids & falls
A. ruthenus	April–June	12.0–17	flooded area	gravel	2.0–15	1.5
A. baerii	May–June	9.0–18 opti: 11–16	main stream	stones, gravel	6.0–8	1.0–4
A. naccarii	Feb–March		middle & lower reaches of the Pô River	along the river banks		low current
A. oxyrinchus	May–June	13.0–18	lower reaches	hard bottom, rocks	11.0–13	0.5–0.8
A. transmontanus	May–June	10.0–19	fast flowing section	cobble, boulders	3.0–23	0.8

yolk-sac resorption, first feeding and active exogenous feeding. Habitat requirements for juveniles change with the seasons. In spring, *A. fulvescens* of the Groundhog River (Ontario) were present predominantly in pools 6–10 m deep; shallows and nearshore areas with high water flows were avoided (juveniles were rarely found at velocities exceeding 70 cm s^{-1}). In summer, lake sturgeon were found in all habitats, however, they were frequently absent from pools in autumn (Seyler, 1999). Studies by Kynard et al. (2000) on the use of large-scale habitat by shortnose sturgeon show preferences for slow water velocities (curves, channels with deep water and sand substrate), reflecting an energy saving strategy in this species. Habitat requirements for each species and life stage should be known prior to substrate manipulation and habitat enhancement in conservation programs.

Karyology and hybridization in sturgeon

Karyotypes of Acipenseriformes are unique compared to those of other vertebrates. The basic chromosomic complement consists of 10 pairs of large sized metacentric chromosomes, 22–25 pairs of small meta-, submeta- and acrocentric chromosomes and 60 microchromosomes, which can easily be mistaken for small fragments of chromatin. This makes the establishment of an exact chromosomal amount almost impossible in octoploid species. Thus, the karyotype may be

Table 5. Acipenseriformes chromosome number (after Birstein et al., 1997b)

Genera	Species	2n chromosomes	pg DNA
Psephurus	*P. gladius*	?	
Polyodon	*P. spathula*	120	3.2–4.9
Huso	*H. huso*	116–118	3.2–3.6
	H. dauricus	120 ?	3.78
Scaphirhynchus	*S. albus*	120 ?	
	S. platorynchus	112	3.6
Pseudoscaphirhynchus	*P. kaufmanni*	120 ?	3.47
	P. hermanni	?	
	P. fedtschenkoi	?	
Acipenser	*A. sturio*	116	3.2–3.6
	A. oxyrinchus	120 ?	4.55
	A. brevirostrum	360 ?–500 ?	13.08
	A. fulvescens	250 ?	8.9
	A. transmontanus	230	9.1–9.6
	A. medirostris	249	8.82
	A. sinensis	264	
	A. schrenkii	240 ?	
	A. mikadoi	500 ?	14.2
	A. gueldenstaedtii	247–256	7.87
	A. stellatus	118	3.74
	A. ruthenus	118	3.74
	A. dabryanus	240 ?	
	A. nudiventris	116–118	3.9
	A. baerii	246–248	
	A. persicus	>200–250	
	A. naccarii	240–250	

better characterized by chromosome banding, *in situ* hybridization with DNA probes, and analyses of synaptonemal complexes (Fontana et al., 1999). Three groups can be distinguished clearly (Table 5): (1) a number of chromosomes close to 2n = 120 (60 macro and 60 microchromosomes and 3.2–3.8 pg DNA); (2) an octoploid with approximately 4n = 240 and twice as much DNA; and (3) measurements of DNA (14 pg) suggest a 16 n ploidy and 500 chrosmosomes (e.g., *A. mikadoi* and *A. brevirostrum*).

Data on nuclear DNA and enzymatic polymorphism suggest that the present Acipenseriformes originated from a tetraploid ancestor that had 120 macro-and micro-chromosomes and DNA content of 3.2–3.8 pg nucleus^{-1}. This was the result of diploidization occurring twice from a common extinct ancestor, which had 60 chromosomes (discussion in Birstein et al., 1993, 1997b; Birstein and DeSalle, 1998). However, for Fontana et al. (1999) the possibility of grouping silver stained NOR chromosomes into pairs and quadruplets, in respectively 120 and 240 chromosomes karyotypes, would support a diploid-triploidy condition in Acipenseriformes. The small level of heterozygosity, the existence of polyploid states, and the presence of a very high microchromosome proportion in association with chromosomes of large size are characteristics found in ancient groups such as lampreys (Petromyzontidae) and suggest that Acipenseriformes are genetically "living Fossils". Indeed, they have existed since at least the Lower Jurassic (200 Million Years BP) in England and Germany (Chondrosteidae) and in the Upper Jurassic/Lower Cretaceous in China (Peipiaosteidae).

Acipenseriformes are characterized by a high capacity for hybridization. In sympatric distribution nearly all species will hybridize. Usually the hybrids 2n × 2n or 4n × 4n (interspecific or intergeneric) are fertile while the interploid crosses 2n × 4n are triploids and are commonly sterile (no oocyte formation in females). In interploid crosses the number of chromosomes is in-between those of the parents, for example, 160–180 in the hybrid *A. gueldenstaedtii* (2n = 240) × *A. ruthenus* (2n = 120). Some caryology parameters, such as the number of bi-armed chromosomes or the number of microchromosomes, are highly variable: CV> 12% compared to 2–4% in the parents (Arefjev, 1999). In the wild, reproductive barriers, which prevent hybridization may be altered by drastic changes in the environment. In the Volga, long-term investigations (1965–1995) showed that the proportion of sturgeon hybrids changes with time. Hybrids reached levels as high as 3.1% of the total migrating juveniles. Among all hybrids the proportion of *A. gueldenstaedtii* × *A. stellatus* was 28% in the 1980s and 56% in 1994. Reduction of available spawning grounds and concentration of the two species on the same spawning sites is the most likely explanation (Lagunova, 1999).

In Russia, hybrids were used in aquaculture to associate complementary parental characteristics. For example, the bester, an intergeneric hybrid between sterlet (male) living in freshwater and beluga (female), is characterized by rapid growth and large size. This hybrid was created in 1952 for rearing in continental waters (at that time it was believed that salinity was required for the growth and maturation of anadromous sturgeon). The hybrid was produced in farms and widely exported. Its karyotype stabilized after the third generation (Arefjev and Nikolaev, 1991) and a decline in progeny survival in the successive generations was reported by Arefjev (1999). It was later found that most of the local species could be reared in freshwater and interest in the bester has lessened (bester represents only 10% of total farm production in Russia, which amounted to 1,200 t in 2000). Many other hybrids were created in Russia: bester × *H. huso*, bester × *A. ruthenus*, *H. huso* × *A. nudiventris*, *A. ruthenus* × *A. nudiventris*, *A. gueldenstaedtii* × *A. ruthenus*, *A. gueldenstaedtii* × *H. huso*, *H. huso* × *A. stellatus* and *A. stellatus* × *A. medirostris* (Krylova, 1999). The offspring of other hybrids performed in-between both parents and not, as often expected, better than the best parent. Thus, there is no clear-cut demonstration of the superiority of hybrids compared to parental performance (growth, food conversion, fecundity, etc.) and the use of hybrids in aquaculture can be questioned, considering the risks of escape into open waters and subsequent genetic contamination of wild sturgeon populations.

Phylogeny

The general morphology of sturgeons is highly characteristic: elongate body with a ventral flat base, rostrum, cartilaginous skeleton, notochord, an intestinal spiral valve, bony dermal plates (scutes) in longitudinal rows on the body, and gill-rakers. The caudal fin is mostly heterocercal (which means asymmetrical, generally with the continuation of the spinal cord in the most developed superior lobe). A generally well-developed spiracle or a vent-hole (post-hyomandibular orifice from which the water is expelled to the upper part of the pre-opercular bone) is present and associated with a pseudo-gill (hyoid arch). This feature is found in every group apart from the Scaphirhynchinae. The central part of the vertebra does not show deformities nor the hemispherical projections found in the teleost group. The premaxillar and the maxillar bones are joined together in the upper jaw and are not attached to the skull. Some of these features were considered primitive characteristics but actually, they are the result of regression such as ossification reduction, absence of teeth (at least in the adult, see discussion in Bemis et al., 1997) and branchiostegal rays. Acipenseriformes also have highly specialized characteristics (rostrum, ventral mouth, barbels). Typically, these general descriptive features are a mix of primitive characters (also present outside Acipenseriformes) and derived ones.

However, if classification has to do with history, taxa must be defined by innovations, i.e., derived characters or synapomorphies (Patterson, 1982a). Such phylogenetic Acipenseriformes signatures and defining clades within the group are summarized and discussed by Grande and Bemis (1991, 1996) and Bemis et al. (1997). Synapomorphies of the Acipenseriformes (including the fossil families Peipiaosteidae and Chondrosteidae) are; (1) the loss of premaxillary and maxillary bones at the lower jaw; (2) the preopercular canal contained in a series of ossicles; (3) the infraorbital sensory canal contained in a series of ossicles; (4) the short mandibular canal or its absence; (5) presence of an anterior process of the subopercle; (6) the gill-arch dentition confined to the first two hypobranchials and to the upper part of the first arch; (7) palatoquadrates with an anterior symphisis, a broad autopalatine portion, palatoquadrate bridge and quadrate flange; and (8) the presence of a triradiate quadratojugal bone. Synapomorphies of the extant Acipenseriformes Polyodontidae and Acipenseridae are; (1) the loss of opercula; (2) the reduction in number of branchiostegals supporting the gill cover; (3) the endocranium with a rostrum; (4) the presence of dorsal and ventral rostral bones; and (5) the ventral process of the post-temporal bone.

Sturgeon are included within the Chondrostei, a clade whose relationships with other actinopterygians are widely accepted (Patterson, 1982b; Lauder and Liem, 1983; Lecointre, 1994; Bemis et al., 1997) and confirmed by molecular data (Lê et al., 1993). Within extant Actinopterygii, the Cladistia (bichirs, Polypteridae) are the sister-group of the Actinopteri. In the Actinopteri, the sturgeons and paddlefishes (Chondrostei) are the sister-group of the Neopterygii. The Neopterygii contains gars (Ginglymodi), the bowfin (Amia) and the Teleostei. The extant Chondrostei include the Acipenseriformes containing two monophyletic families: the Polyodontidae and the Acipenseridae. Grande and Bemis (1996), Bemis et al. (1997) and Birstein and DeSalle (1998) gave complete phylogenies of the Acipenseriformes, including fossils, and made nomenclatural recommendations. A consensus tree taking into account recent syntheses (Bemis and Kynard, 1997) and molecular phylogenies (Birstein and DeSalle, 1998; Krieger et al., 2000) is given in Figure 3. In the extant Polyodontidae (2 species), the monospecific genus *Psephurus* is the sister-group of the monophyletic *Polyodon*.

In the monophyletic family, Acipenseridae, the four extant genera are monophyletic, with a possible contradiction from molecular data concerning the respective monophylies of *Huso* and *Acipenser* (see below). From morphological data, *Scaphirhynchus* is the sister-group of *Pseudoscaphirhynchus*, and both are included in the Scaphirhynchini (Grande and Bemis, 1996). The Scaphirhynchini is the sister-group of the genus *Acipenser*; both are included in the Acipenserinae. The Acipenserinae is the sister-group of the genus *Huso*. Morphologists consider *Huso* as the sister-group of all other Acipenseridae. However, Birstein and DeSalle (1998) found a strong molecular signal grouping *Huso* and *Acipenser ruthenus*. In their phylogeny, resulting from a combined weighted parsimony analysis of both cytochrome b and 12S–16S mitochondrial sequences, *Huso* is paraphyletic with *Huso huso* as the sister-group of *Acipenser ruthenus*. The genus *Acipenser* is, therefore, also paraphyletic (except if we now consider *Huso* as real paedomorphic *Acipenser*).

This contradiction may have an explanation. If *Huso huso* and *Acipenser ruthenus* are considerably different in general morphology and ecology, they do hybridize and hybrids are not only viable but also fertile (Birstein et al., 1997b). It is still possible that the two species of *Huso* that were sampled by Birstein and DeSalle (1998) were not 'pure' *Huso* mitochondrial strains. Original sample populations might have retained mitochondrial genomes from *A. ruthenus*. The nodes grouping *Huso* and *A. ruthenus* have relatively good support, but would result from the history of genes, not from the history of species (Doyle, 1992, 1997; Maddison, 1997). Even if *A. ruthenus* and *H. huso* populations are now isolated in the wild, the generation time is so long in sturgeon, particularly in *H. huso* (Table 2), that such mitochondrial signals of introgressive hybridization could be remnants of very ancient times. This is favored by possible recent bottlenecks in populations, during which a mitochondrial lineage may become fixed (for example *A. ruthenus* haplotype becoming the dominant one in cells of *Huso huso*). One hypothesis (Doyle, 1992; Maddison, 1997) is that, if a pure *Huso* mitochondrial lineage was sampled, *Huso* could have appeared as the sister-group of all the *Acipenser* species. This hypothesis is worth testing by investigating the phylogenetic relationships of *Huso* from a nuclear gene.

The Polyodontidae do not have rows of shields but are totally covered by small scutes and have a long flattened rostrum widening at its extremity (spatula). The Polyodontidae family is composed of two genera: *Polyodon* (Lacepède, 1797) with only one species, *P. spathula* (Walbaum, 1792) living in freshwater in the eastern regions of Northern America (Mississippi) and *Psephurus* (Gunther, 1873) with *Psephurus gladius* (Martens, 1862) living in the Chang Jiang (Yangtze) River in China. The gill rakers of *Psephurus gladius* are short and less numerous than those of *Polyodon spathula*.

The Acipenseridae have a shorter rostrum than that of the Polyodontidae. They have 5 longitudinal rows of well-developed bony shields; one dorsal, two lateral, and two ventral. Spikes on the shields are sharp in the young and blunt in the adult. The number of shields is specific for certain species. The skin is covered by bony plates and the first ray of the pectoral fin is transformed into a spine. The lower jaw is protractile, and the adults have no teeth. The mouth is surrounded by thick lips and has a row of 4 barbels in front. The number of gill rakers is reduced and the branchiostegal bone (located under the lower jaw for teleost fish) is absent. Gills are covered by a thick bone, the sub-operculum, and the

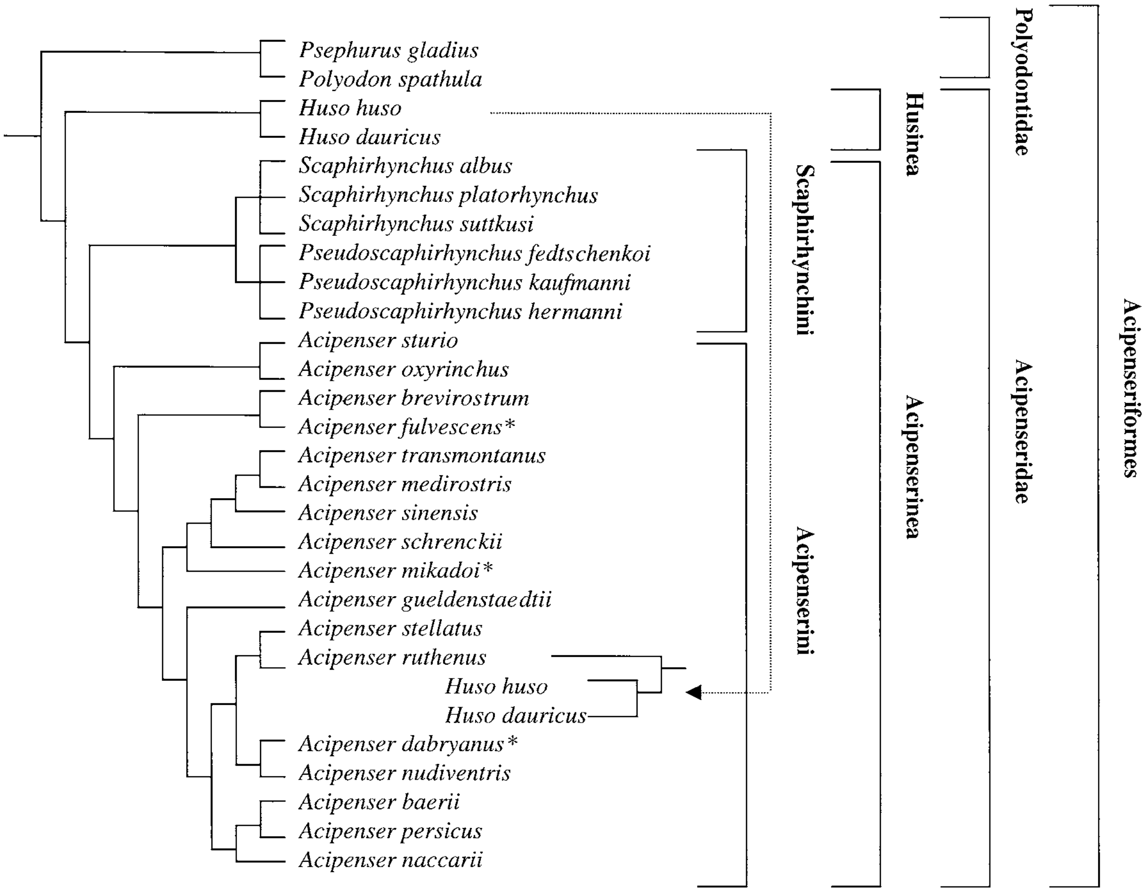

Figure 3. Interrelationships of extant acipenseriformes based on the consensus tree of Bemis and Kynard (1997) with alterations made from new molecular data ∗ (Birstein and DeSalle, 1998; Krieger et al., 2000). When possible, multifurcations were resolved following statistically supported nodes, from the molecular analysis of Birstein and DeSalle (1998). Right dotted line: molecular alternative for relationships of *Huso, which* was placed in the genus Acipenser by Birstein et al. (1999).

classic opercular bones of bony fish are either diminished (pre-operculum), or absent (inter-operculum or operculum).

The Acipenseridae may be divided into three subfamilies; Husinae (Findeis, 1997), Acipenserinae including the Scaphirhynchini (Grande and Bemis, 1996), and Acipenserini (Figure 3). The Husinae (Acipenserini of Bonaparte, 1845) have a conical rostrum more or less pointed with rounded edges, a well-developed spiracle and a caudal fin with no strand. Currently, two genera have been acknowledged: *Huso* (Brandt, 1869) has a large mouth that opens towards the back in the shape of a crescent, and a branchial membrane unattached to the isthmus (under the lower jaw); *Acipenser* (Linneus, 1758) has a smaller mouth, which is transversal and rectilinear, and a branchial membrane, which is attached to the isthmus. However, the genus *Huso* has been questioned on the basis of molecular data. But, as long as the recent molecular results of Birstein and DeSalle (1998) remain unconfirmed by nuclear genes, the genus *Huso* can be kept provisionally.

The Scaphirhynchines (Bonaparte, 1845) have a rostrum that is slightly flattened into a spatula with sharp edges. They do not have a vent-hole (spiracle) and the upper lobe of the caudal fin is extended by a long, thin strand. Two genera have been identified: *Scaphirhynchus* (Haeckel, 1835) and *Pseudoscaphirhynchus* (Berg, 1904). *Scaphirhynchus* is characterized by fringed barbels, its long caudal peduncle, which is entirely mailed (totally covered with shields), and a long anal fin whose extremity reaches the caudal base. Three species of this genus exist: *S. platorynchus, S. albus* and *S. suttkusi* (Bailey and Cross, 1954;

Williams and Clemmer, 1991; Mayden and Kuhajda, 1996). *Pseudoscaphirhynchus* is characterized by a caudal peduncle not entirely covered by shields, a short anal fin that does not reach the base of the caudal fin, and either smooth or partly fringed barbels.

The species and their present threatened status

A brief description of some biological features plus the present threatened status and conservation measures already taken or recommended are given for each species of Acipenseridae and Polyodontidae. Conservation is used in the sense of keeping sturgeons as sustainable resources as defined by Bartley (1998), "conservation is a dynamic process where resources are maintained or managed so that they can be utilized at future points." Status is mostly derived from proposals submitted by the sturgeon specialist group of the UICN (Birstein et al., 1997c). Available information on biology, population structure, stocks, and habitat to be rehabilitated is very different among species and is extremely limited, particularly for critically endangered groups such as *Pseudoscaphirhynchus*, *Scaphirhynchus* and *Psephurus*. This paucity of information is mostly due to the lack of specimens for research. Information on stocks and on the efficiency of conservation measures is not always accurate. However, the regulation of the international trade in Acipenseriformes by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 1994/98/99) represents a major international action. This includes recommendations for a series of measures to be taken to ensure effective management of wild populations of Acipenseriformes, including the establishment of annual export quotas for specimens, parts, and derivatives of species.

Sturgeon are adversely affected by degradation of habitat and water quality, and accumulation of toxic compounds in sediments and in the trophic web. Sturgeons are sensitive to toxic pollutants accumulated in the sediments due to their benthic feeding habits and late puberty, which increases bioacccumulation in the various tissues (muscles, fat, gonads, etc.). The species are listed according to their threatened status in descending order. The order of a species having several populations of differing status is based on the threatened level for the majority of the populations. For instance, *A. nudiventris* has several populations: most are Endangered, one is Critically Endangered and one is Extinct. Thus, *A. nudiventris* is placed in the Endangered group.

Critically Endangered

Pseudoscaphirhynchus fedtschenkoi (Acipenseridae) Syr-Dar shovelnose sturgeon

Distribution
Lives in an endemic state in the lower and middle reaches of the Syr-Darya River but historically was found in the Aral Sea. This is no longer possible because the river (from which 70% of the water has disappeared) sometimes does not reach the sea and salinity in the Aral Sea is now too high (37–38‰ compared to 10‰ in 1960).

Identification
Historically three morphs were identified by Berg (1948); (1) common morph with a long caudal filament, (2) morpha brevirostris with short snout and long caudal filament, and (3) morpha intermedia with middle-sized snout and a filament. Medium-sized (maximum 65 cm); it is essentially a freshwater morph.

Habitat and reproductive characteristics
Adults are benthophagous, feeding on midge larvae. Spawning commonly takes place during late April.

Stock status and conservation measures
Does not have any commercial value. Is on the verge of becoming extinct due the obstruction of migration trails and water and sediment pollution. It was considered extinct by Pavlov et al. (1994) and Zholdasova (1997) but specimens were recently seen in the Karakum Canal (Birstein, 1997). Currently, it receives no protection although the species is on the KazakSSR (1968), the USSR (1983) and IUCN Red Data Books.

Pseudoscaphirhynchus hermanni (Acipenseridae) small Amu-Dar shovelnose sturgeon

Distribution
Present in the lower and middle reaches of the Amu-Darya and has historically frequented the Aral Sea.

Identification
Morphology is similar to *P. kaufmanni* but smaller at 21–27 cm and different to any of the forms of

P. fedtschenkoi (Findeis, 1997); it has a longer snout and is deprived of caudal filament.

Habitat and reproductive characteristics
Adults are benthophagous and feed on midge larvae. All *Pseudoscaphirhynchus* demonstrate benthic morphology with a flattened head, which is among the most prominent in the Acipenserids (Findeis, 1997). According to most authors this species is rare. It can hybridize with *P. kaufmanni*.

Stock status and conservation measures
Historically rare. Specimens were captured 10 years ago and 3 were caught in April 1996 (Birstein, 1997). Critically endangered, it is on the UzbekSSR (1994) and TurkmenSSR (1985) Red Data Books. Threatened by construction of dams and channels (both changing the water regime) and from pollution in the Syr Darya (Birstein, 1997); no protective measures known.

Psephurus gladius (Polyodontidae) Chinese paddlefish

Distribution
The Chinese paddlefish lives on the riverine bottom of the Yangtze (Liu Chenhan et al., 1995); historically, it occurred in the Yellow River and the Yellow Sea (Li, 1965) and in the Chinese Sea suggesting anadromy or freshwater amphidromy (Bemis and Kynard, 1997). Sympatric with *A. sinensis*.

Identification
Paddlefish are thought to be closely related to *Acipenser* on the basis of similarities in the karyotype (shape of the chromosomes) and the presence of a coelenterate parasite on the gonads in both families. Compared to Acipenseridae the heterocercal characteristic of the caudal fin is less pronounced (but like all Acipenseriformes, the spinal cord is prolonged in the superior lobe of the caudal fin). The Chinese paddlefish remains poorly studied and its relationships with other groups are not well understood (Bemis et al., 1997). This is the biggest freshwater fish in China but it probably never reached 7 m in length (Nichols, 1943) and 500 kg (Wei et al., 1997). However, Liu Chenhan et al. (1995) report sizes of 3 m and 300 kg.

Habitat and reproductive characteristics
The Chinese paddlefish is piscivorous, contrary to the other paddlefish, *Polyodon spathula*, although both species have a spatula. Precise migration patterns and spawning sites are unknown. Spawning occurs in April at 18–20 °C, at a water flow rate of 0.72–0.94 m s^{-1}, and at a depth of 10 m; egg diameter is 2.8–3.8 mm according to Wei et al. (1997) or 2.0–2.4 mm for Liu Chenhan et al. (1995).

Stock status and conservation measures
Stocks were low historically (annual captures of 25 t before 1976, very low afterwards) and are threatened due to water pollution and dam construction (e.g., the Gezhouba Dam which prevented upstream migration). Few adults have been found below the dam since 1988. Limited spawning was observed above the dam but this spawning area is now threatened by the Three-Gorge Dam. Fully protected in China since 1983. Protection zones were established and fishers were encouraged to release by-catch paddlefish. Those measures were obviously not effective as the species is on the verge of extinction and will disappear from the middle and the lower reaches of the Yangtze according to Wei et al. (1997) and Birstein (1997). The potential for farm production of this species has been discussed by Mims et al. (1993). However, Wei et al. (1997) found it difficult to keep the adults in captivity and to date artificial spawning has been unsuccessful.

Scaphirhynchus suttkusi (Acipenseridae) Alabama sturgeon

Distribution
A new species of freshwater sturgeon was recognized by Williams and Clemmer (1991) in the "Mobile Basin" of the Mississippi and the Alabama Rivers from 32 specimens gathered over a century that were either not identified or misidentified. The species was last captured in 1985.

Identification
S. suttkusi closely resembles the shovelnose sturgeon morphologically but differs significantly in 6 meristic characters and at least eleven measurable variables. Comparison with other species using PCR products has shown a degree of genetic differentiation between *S. suttkusi* and the two other *Scaphirhynchus* which was greater than that of *A. oxyrynchus* and less than that of *A. fulvescens* and *A. oxyrynchus* (Wirgin et al., 1997). The Alabama sturgeon reaches lengths between 36 and 72 cm and the maximum weight is 2.3 kg (Williams and Clemmer, 1991).

Habitat and reproductive characteristics

Based on limited data from a few captured individuals, the Alabama sturgeon is found in large coastal plain rivers in large unmodified river channels in moderate to swift currents, at depths of 6 to 14 m over sand and gravel or mud bottoms. Feeding regime is based on macroinvertebrates, occasionally small fish, plant items, mollusks and snails in sandy depositional areas with little silt and slow to moderate current (Mayden and Kuhajda, 1997). Spawning occurs on relatively stable rock or gravel substrates in tributaries of large rivers. Like other *Scarphirynchus*, it spawns in freshwater in spring and early summer (probably from February to July, spawning runs being triggered by rising water levels in spring and summer); it is sexually mature at 5–7 years of age.

Stock status and conservation measures

Extremely rare. For the last century its area of distribution has been considerably reduced by anthropogenic changes to ecosystems such as the damming of rivers causing changes in river channels and water flow patterns. It is not extinct. Two adult specimens were captured in 1995 and 1996. Mayden and Kuhajda (1996, 1997) gave some general conservation measures and recommendations. These include: (1) maintain appropriate spawning habitats; (2) increase access to upstream and downstream river stretches across dams; (3) establish minimum flow regime; and (4) decrease silt load. It is recognized as the most endangered species in the USA but received no protection until it was listed by USFWS in 2000. The listing has been charged with strong political and industrial opposition related to potential environmental regulations for the users of the large rivers inhabited by this species (Mayden and Kuhajda, 1997).

Acipenser dabryanus (Acipenseridae) Dabry's sturgeon

Distribution

This species lives in freshwater and is found in the Yangtze in China, and in the Tungting Lake (Hunan). Historically, it was also seen in freshwater in Korea but is now restricted to the Yangtze. It is partially sympatric with *A. sinensis*. It is freshwater amphidromous or potamodromous (Bemis and Kynard, 1997).

Identification

It is rare, not well known and the population has always been small. Relatively small in size: 130 cm, 16 kg it is restricted (landlocked) to the reaches of the main stream above the Gezhouba Dam (Wei et al., 1997).

Habitat and reproductive characteristics

The young eat zooplankton, oligochaeta and small fish. Males start to mature at the age of 4 (4–5 kg) females at 6 (>9 kg). It does not migrate (except for spawning) and lives in various habitats, but prefers a sandy bottom with silt grounds, water velocities of 1.2–1.5 m s^{-1}, and a water depth of 5–15 m. When the water level rises in the main stream in spring these sturgeons move to the tributaries to feed and possibly to spawn. Stock status and conservation measures The Chinese are trying to reproduce it artificially and there is an urgent need for protection because it is at a high risk of extinction (Zhuang et al., 1997).

Acipenser sturio (Acipenseridae) European Atlantic sturgeon, common sturgeon

Distribution

A. sturio is present in the Gironde, the Atlantic and the North Sea. Rochard et al. (1997) recorded 179 incidental catches of young specimens (average length 113 cm) of *A. sturio* from the Bay of Biscay to Scandinavia, including estuaries in England and in the Rhine in Holland. It may be present in the Rioni and the Black Sea as a relic population. Its geographic distribution used to be much larger. Debus (1995) reviewed the historic and recent distribution in the Baltic Sea and a specimen was caught in 1996 (Paaver, 1999). Bloch (1785), gave a wide distribution for this species: the North Sea, the Mediterranean and the Black Seas, and in numerous rivers, the Elbe, the Oder, the Spree in Berlin, the Nile, the Gironde and even in the Volga River. This sturgeon is not usually reported in the Volga so there was probably some confusion with other Ponto-Caspian species which had not been identified at that time (with the exception of *H. huso* L. 1758 and *A. ruthenus* L. 1758). As the Ponto-Caspian ichthyofauna shows some similarities (due to shared inhabitance of the Paratethys Sea during the Pliocene) we would expect *A. sturio* to be present in the Caspian Sea, unless a later colonization restricted to the Black Sea occurred from the Mediterranean Sea.

Identification
Debus (1999) found some differences in the bony plates of the Baltic sturgeon compared to *A. sturio* from La Gironde and the Rioni Rivers but concluded that only one species is present in European waters. Birstein et al. (1998) have amplified a partial sequence of cytochrome b on six specimens caught recently in the historical range of *A. sturio*; four individuals (one from the North Sea, one from the Baltic and two from La Gironde) were identified as *A. sturio*, and two as a clade of fish including *A. naccarii* and *A. baerii*. Since different *A. sturio* populations are present, the authors urge colleagues involved in restoration work to identify their sample material carefully. The North American and the European sturgeons were long considered two sub-species of *A. sturio* L (1758): respectively, *A. sturio oxyrinchus* and *A. sturio sturio*. They were separated into two species (*A. oxyrinchus, A. sturio*) on the basis of morphological and meristic characters by Vladykov and Greeley (1963). This was first supported by molecular analysis (Wirgin et al., 1997; Birstein and DeSalle, 1998), but Artyukhin and Vecsei (1999) proposed four geographic forms of a single species of *A. sturio* from morphological and biological features: *A. sturio oxyrinchus* Mitchill, 1814 (North American watershed), *A. sturio sturio* L (1758) (Baltic Sea, North Sea), *A. sturio occidentalis* (subspecies nova, Gironde, Iberian Peninsula, Mediterranean Sea, Black Sea) and *A. sturio de sotoi* (Vladykov, 1955) (Gulf of Mexico).

Habitat and reproductive characteristics
A. sturio is an anadromous species that tolerates full salinity (35‰ salt-water), at least for the Atlantic population. A freshwater form has existed in the Ladoga Lake. The capacity to adapt itself to high salinity is acquired slowly. Magnin (1962) reported that two-year-old subjects can withstand salinities of 3 to 8‰ but die in full seawater. Four-year-old subjects can be directly transferred to 33‰ salinity. Feeding regime is mostly based on zoobenthos (annelids, crustaceans, mollusks) and fish. *A. sturio* can accomplish long migrations, up to 1,000 km in rivers, to reproduce. Out at sea, the migrations are more limited and the depths at which the sturgeons are caught never exceed 100 m; they seem to stay on the continental shelf and move along the coast.

Stock status and conservation measures
Natural reproduction in the wild (La Gironde) was observed in 1988 and 1995, and artificial reproduction was obtained with wild spawners in June 1995 by the Cemagref team from Bordeaux. Some 2,000 juveniles were released in La Gironde and some were grown in captivity (Williot et al., 1997). Highly protected in France, since 1982; fishing, transportation and trade are strictly prohibited. Strong financial efforts to rehabilitate it in La Gironde are supported by the European Commission (program LIFE, EC) and national and local authorities.

Endangered

Huso dauricus (Husinae Acipenseridae) kaluga

Distribution
This species is endemic in the Amur Basin where Krykhtin and Svirskii (1997) recognized four populations. Two are exclusively freshwater and stay in the rivers, one in the lower part and the other in the middle part; one is anadromous, and migrates into the Gulf of Amur (individuals enter the Okhotsk and Japanese Seas); one is restricted to the lower reaches of the Zeya and Bureya Rivers. Certain members of the species live in the rivers of the Sakhalin Islands. These fish are smaller than those of the Amur River.

Identification
Along with *H. huso*, the kaluga is one of the biggest freshwater fish. Some specimens caught in the past reached 1 t in weight and more than 5.6 m in length and brood fish still reach weights of 200 to 250 kg at the age of 30 according to Krykhtin (1976) and 500 kg (3 m) at the age of 40 according to Wei et al. (1997). The kaluga has a large mouth that occupies the total width of the ventral part of the head.

Habitat and reproductive characteristics
These fish become piscivorous very early and show pelagic habits in the sea. Spawning occurs in May–June at 15–20 °C in upstream rivers, in calm waters, on gravel bottoms. Hybrids between *A. schrenckii* and *H. dauricus* are sterile (the number of chromosomes is different in the 2 species).

Stock status and conservation measures
Its population has never been very large (Wei et al., 1997). Commercial fishing of *A. schrenckii* and *H. dauricus* is still active with 2–5 fishing boats per km in the middle reaches of the Chinese side of the Amur River. Partial statistics for both species indicate capture of 70–80 t year $^{-1}$ in 1950 and 200 t in 1987

with caviar exports of 3 t in 1970 and 10 t in 1990. While it was over-fished, because its caviar is valued, it now benefits from protective measures, which are still insufficient and should be extended on an international level (with Russia) taking into consideration poaching activity and dam construction projects. Presently there are no serious protection measures. The general recommendations of Wei et al. (1997) are: modification of the existing fishing regulations, reduction of fishing pressure including restriction in the number of boats and gears, limiting the maximum allowable catch, banning fishing of juveniles, and strengthening artificial propagation and research on stocks.

Huso huso (Husinae Acipenseridae) beluga

Distribution

H. huso is a diadromous species whose trophic phase takes place in the Black, Caspian and Azov Seas while the reproductive and juvenile phases occur in freshwater in large rivers. Bloch (1785) reported *H. huso* in the Pô and in the Mediterranean Sea and in the Danube near Vienna or Linz. Hensel and Holcik (1997) mentioned that, historically, the beluga was among the most abundant of Danubian anadromous fish. Populations or races (natio) are present in each of the large rivers: Volga, Ural, Kura, Danube and the Dniepr and all populations are mixed on their feeding grounds in the sea. In the Caspian Sea the beluga lives in deep areas in winter (below 30 m), ascends to the 10–20 m zone in spring, and is distributed throughout the whole SE region by summer. In autumn it migrates to feeding in zones south of the Gasan-Kuli-Aster line. *H. huso* is sympatric with *A. gueldenstaedtii, A. stellatus* and *A. nudiventris*.

Identification

The beluga is the largest sturgeon in European waters. Because it is piscivorous, the mouth is protractile in the shape of an inverted half-moon; the middle of the lower lip is crescent-shaped.

Habitat and reproductive characteristics

In the Caspian Sea the diet is principally composed of fish: the common kilka herring (*Clupeonella* spp.) for small belugas under 40 cm, diverse Gobidea for those ranging between 40 and 280 cm and mullets, shad (*Alosa* spp.) and other sturgeons for the biggest (Filippov, 1976). In estuaries and rivers, migrating spawners eat various cyprinids (common carp (*Cyprinus carpio*), roach (*R. rutilus*)), zander (*Stizostedion lucioperca*) and *A. ruthenus* (Sokolov, in Holcik, 1989). Khodorevskaya et al. (1995) have studied the food content of the digestive tract and found both a great diversity of captured prey (73% fish) and varying stomach fullness according to the stage of migration. The spawners migrate upstream in fall, live in deep zones throughout winter and spawn in spring on deep pebble bottoms with rapid currents. Certain populations only go upstream in spring and spawn during the same season. Spawning requires a strong river flow rate (25,000 $m^3 s^{-1}$) for 15–20 days (Novikova, 1994).

Stock status and conservation measures

Captures have been greatly reduced during the last 30 years, from 18,000–26,000 t in 1970, to 14,000–16,000 t in 1986–1987 and less than 1,000 t at the end of the 1990s. The estimated total number of belugas in the Caspian Sea was 21 million in 1988, 15 in 1991 and 8.9 in 1994 (Khodorevskaya and Krasikov, 1999). Raspopov (1993) considered that most recently captured females were in their first year of maturation. While the Volga's populations are reduced, the Ural's remain abundant (there is no dam on this river) but stricter regulation of fishing is needed. Juveniles are stocked in the Caspian and Azov seas. This species needs strong international measures of protection; it was listed "Vulnerable and Endangered" by Lelek (1987). The population of the Adriatic Sea is extinct and all other populations are in danger. The population of the Azov Sea is critically endangered (two mature specimens were caught in the Kuban River in 1999 and none in 2000). Captive brood stocks are available at the Kraznodar Research Center and the production of juveniles for stocking still takes place.

Pseudoscaphirhynchus kaufmanni (Acipenseridae) large Amu-Dar shovelnose sturgeon

Distribution

Until the 1960s it inhabited the entire Amu-Darya River and could be found in the estuary zones in the Aral Sea (it can tolerate 8.5‰ salinity). After 1960 it was restricted to the middle reaches. Essentially freshwater, these fish prefer shallow (1–2 m deep) turbulent waters with a fast current, on a sandy or a stony-pebble bottom or the edges of pools with turbid waters (Zholdasova, 1997).

Identification
Historically, the maximum size was 75 cm (total length, including the long caudal strand) and 2 kg. In the early 1960's the average size recorded was 37 cm, 241 g (age 1+ to 14+) and two forms were recognized (common and dwarf). For dwarf adults, the dorsal, anal and ventral fins are closer to the tail compared to the common form (Birstein, 1997). When the lower parts of the Amu-Darya became inhospitable, and as there was no access to the Aral Sea, migrating forms (which were bigger) vanished and only dwarf forms remained in the middle part of the river (Birstein, 1993). The males have a larger snout than the females. It easily hybridized with the two other *Pseudoscaphirhynchus* in the past.

Habitat and reproductive characteristics
Adults are benthophagous and piscivorous. Their feeding regime has changed, the content of fish in the diet was 64% in 1960 and 37% now, while the amount of chironomid larvae has increased accordingly (Zholdasova, 1997). Adults spawn in spring. Juveniles stay in the bed of the river, first eating insect larvae and later small fish (loaches such as *Noemacheilius oxianus* and species of the genus *Rhynogobius*).

Stock status and conservation measures
The species was commercially exploited in the 1930s. It is of interest for aquariums; some living individuals are found at the Moscow aquarium. It is on the IUCN Red list 1996. An international recovery project is planned (Birstein, 1997).

Scaphirhynchus albus (Acipenseridae) pallid sturgeon

Distribution
Restricted to freshwater, this sturgeon lives in the middle and upper parts of the Mississippi, Missouri and Yellowstone Rivers of North America, on hard bottoms with a strong current and high turbulence. The total historic range was 6,200 km of these large rivers (Keenlyne, 1995).

Identification
It was recognized as a species in 1905 by Forbes and Richardson and was never separated from the sympatric species *S. platorhynchus* when captured. It is not abundant and is not very well known. Pallid sturgeon may weigh up to 45 kg and reach 40 years of age.

Habitat and reproductive characteristics
This fish mostly feeds on aquatic insects (trichoptera) and small fish (cyprinids) (Carlson et al., 1985). In captivity they are successfully fed goldfish, crayfish and minnows. The males reach puberty at the age of 5–7 and the females show some development of oocytes by the age of 9–12 but reproduce for the first time at the age of 15 (Keenlyne and Jenkins, 1993; Keelyne, 1995). Intervals occur between spawning, 2–3 years in males and 3 to 10 years in females (Mayden and Kuhajda, 1997).

Stock status and conservation measures
The species is protected (listed endangered in 1990) in the following states: Arkansas, Illinois, Iowa, Kansas, Missouri, N. Dakota, Tennessee and is in decline in the rest of the USA. The risks that affect this species are primarily pollution in sediments, habitat modifications, poaching and illegal caviar production, accidental capture by fishermen and the development of sport fishing. Another concern is that hybridizations were recently observed due to anthropogenic changes to the environment (Carlson et al., 1985) but Mayden and Kuhajda (1997) found no evidence of hybridization. A recovery plan involves the protection and the restoration of sturgeon habitat (Graham et al., 1995).

Acipenser nudiventris (Acipenseridae) ship sturgeon

Distribution
Most populations stay in rivers for long periods. In the Danube some forms are entirely freshwater dwellers. The species was common to the basins of the Aral and Caspian Seas and more rare in the Azov and Black Seas. In 1863 a specimen was sighted in the Danube River at Bratislava (river km 1869). It is rarely reported in the lower Danube (Bacalbasa-Dobrovici, 1999; Hensel and Holcik, 1997).

Identification
The ventral shields on this sturgeon disappear with age (hence the name nudiventris). In the Kura River, where a specimen of 160 cm and 45 kg was reported by Zholdasova (1997), the females are bigger than the males, 175 cm against 141 cm for individuals of the same age.

Habitat and reproductive characteristics
In the Ural, it was estimated that 3,500–5,000 mature spawners reproduce each year. It is much les now,

290 t caught in 1999. Out at sea this species lives by the coast in muddy depths, which do not exceed 50 m.

Stock status and conservation measures
In the Caspian Sea it is over-exploited and juveniles are sold as aquarium fish. Protection measures are needed, including a total ban of fishing. The Aral Sea population is extinct (Zholdasova, 1997). Most populations are listed as Endangered but some, as in the Danube River, are listed as Critically Endangered. The native sturgeon population of the Syr-Darya was transplanted to lake Balhash and acclimatized in the 1960s where is still exists (this was one of the few successful acclimatizations of a sturgeon species out of its distribution range; see also Zakharov et al., 1998 and Tsvetnenko, 1993). There is a project to bring the sturgeon back to the Aral Sea.

Acipenser sinensis (Acipenseridae) Chinese sturgeon

Distribution
This Asian species is found in the Yangtze, the Pearl Rivers and in the Min and Lia-ho Rivers in N-E China (Wei et al., 1997); it is sympatric with *A. dabryanus*. *A. kikuchi*, first described as a Japanese species, was recognized by Takeuchi (1979) as being *A. sinensis*.

Identification
The morphology of the Pearl and Yangtze River populations is different but it is not clear if they are separate sub-species.

Habitat and reproductive characteristics
A. sinensis is anadromous. Growing fields are found in the Chinese Sea and the Yellow Sea, the south of Korea and the south of the Japanese Sea. In the Yangtze, the maturing sturgeons migrate in June-July from the sea towards the lower parts of the river where they spawn in October-November (an unusual time for most fish in the northern hemisphere). *A. sinensis* eggs are large, up to 5 mm (the largest in sturgeon), but the water temperature is high 15–20 °C and hatching occurs within 130 hours. The young are free-swimming until the winter but there is no information on their habitat and feeding during the cold season. Juveniles of 7–38 cm TL (presumably one year old) reach the Yangtze estuary in the middle of April (Wei et al., 1997).

Stock status and conservation measures
Since the beginning of the 1980's the Gezhouba Dam has prevented spawners from moving up the Yangtze and some reproduction takes place below the dam. In addition, this spawning area is badly damaged due to gravel and rock extraction for the construction of the Three Gorge Dam. The fry are concentrated downstream, over an area of 20 km. The number of sturgeon has always been low and specimens are becoming rare. This species needs urgent protection measures. Breeding attempts are being made in order to restock the population. The release of 2.8 million larvae and 17,000 juveniles (2–10 g) occurred 1983–1993. Commercial fishing has been prohibited since 1983. Wei et al. (1997) recommended the establishment of a protected area for juveniles at the Yangtze estuary, creation of additional artificial spawning areas below the dam, and collection of more information about the biology, migration and spawning sites.

Acipenser schrenckii (Acipenseridae) Amur sturgeon

Distribution
This is the main endemic sturgeon species in the Amur Basin from the mouth to the upper middle reaches and in a tributary of the Issury River. Spawning sites are known to exist in the mouth of tributaries in the upper-middle reaches (Wei et al., 1997).

Identification
Krykhtin and Svirskii (1997) recognized 2 morphs, one brown (middle and lower reaches) and one grey, whose distribution and spawning sites are the same as for *H. dauricus*. Inter-morph crosses result in 2–5% hybrids. The grey morph can reach 3 m, 190 kg at 60 years of age; it lives principally in freshwater. Populations have been sighted living in the brackish waters of liman (lagoons) at the mouth of the Amur River.

Stock status and conservation measures
Fishing is prohibited in the Amur Basin except from June 15th to July 15th where the limit is 60 t (for *A. schrenckii* and *H. dauricus* together). Chinese fishermen alone have caught approximately 410 t of both species in 1989 and 170 t in 1993 (Krykhtin and Svirskii, 1997). International trade is illegal. This species is affected by water and sediment pollution, dam construction, and poaching on the Russian side, particularly during the spawning migrations and on the

spawning grounds. International measures of protection are necessary in this threatened species. The present population in the lower Amur River is estimated at 95,000 fish over 2 years of age. That is half as large as the population of the middle Amur River. Wei et al. (1997) recommended reducing the fishing effort, strictly forbidding the capture of juveniles and strengthening artificial propagation in the Amur River (for both *A. schrenkii* and *Huso dauricus*). A joint conservation effort is needed in the shared waters of Russia and China. The culture of Amur sturgeon started in the 1950's and intensive production is now planned (Zhuang and Yi, 1999). A propagation station was set up in 1988; 900,000 larvae (0.2–0.4 g) and 168,000 juveniles (up to 30 g) were released from 1988 to 1991.

Acipenser multiscutatus, was observed by Okada (1959–1960) off Iwaki, East of Japan. Its status was controversial and Artyukhin and Andronov (1990) wonder why this species only exists in Japan and not on the North Asian continent. Japanese rivers are of moderate size and, since this fish is large (2–3 m), it cannot live exclusively in freshwater. It is probably anadromous and should have reached the Asian continent. *A. multiscutatus* is probably synonymous with *A. schrenkii* for Birstein and Bemis (1997) but their physiology is different. *A. schrenkii* lives predominantly in freshwater.

Acipenser mikadoi (Acipenseridae) Sakhalin sturgeon

Distribution

A. mikadoi is located in the North Asian Pacific (the Sea of Japan to the Korean Peninsula, the Japanese rivers of Hokkaido, the basin of the Amur River, and the Tumnin River, which is the only spawning area known in Russia).

Identification

This species is sometimes grouped with *A. medirostris*. However, it has a greater number of rays on its dorsal and anal fins, more lateral shields, less ventral shields and important quantitative differences are found in the nuclear DNA. Birstein et al. (1997b, 1993) found that the Asian form, *A. mikadoi*, has a larger amount of nuclear DNA (14.2 pg) than *A. medirostris* (8.82 pg) and suggested that they are two different species, an idea first proposed by Hilgendorf (1892). Molecular data on three mitochondrial genes also showed differences between the two groups (Birstein and DeSalle, 1998).

Stock status and conservation measures

This species spawns in small rivers and consequently there is a concentration of immature fish in the lower part of the river and in the estuary (Artyukin and Andronov, 1990). It is now rare and receives no special protection. It is rare in Japan and is on the Red Book of the USSR (Pavlov et al., 1985, 1994).

Acipenser gueldenstaedtii (Acipenseridae) Russian sturgeon

Distribution

This diadromous species is found in the rivers running to the Azov Sea (Don, Kuban), the Black Sea (Danube, Dniepr, Bug, Dniestr, Rioni, Inguri) and the Caspian Sea (Volga, Ural, Kura, Terek, Sulak). A landlocked population of *A. gueldenstaedtii* is still present above the Iron Gates Dam on the lower Danube (Hensel and Holcik, 1997).

Identification

Several infraspecies forms were proposed but they were found invalid by Birstein and Bemis (1997). *A. gueldenstaedtii* is sympatric with *A. stellatus, A. nudiventris* and *H. huso*. Frequent crosses exist between these populations, sub-species and species. Viable hybrids are reported with *A. stellatus, A. sturio, A. nudiventris* and *H. huso*.

Habitat and reproductive characteristics

The Russian sturgeon is a bottom-dwelling mollusk feeder. In the Caspian Sea the diet consists of mollusks and fish (Polyaninova and Molodtseva, 1995), but its characteristic diet has varied with time (e.g., the increase of *Nereis diversicolor* in the stomach contents after its introduction in the Caspian Sea at the end of the 1930s and the appearance of the crab (*Rhitropanopeus harrisii*) at the end of the 1950s). The contribution of natural reproduction to stock recruitment was reduced after the Volga River flow regulation in 1959; the biomass of spawners was 7,500 t in 1960, 3,000 t in 1981–1985 and 830 t in the early 1990s (Khodorevskaya et al., 1997). In the unregulated Ural River, the spawning grounds are located 900 to 1,200 km from the sea for the winter race and 320–650 km for the spring race. Spawning takes place at a temperature of 8–15 °C and a water velocity of 1–1.5 m s^{-1}.

Stock status and conservation measures
In the northern part of the Caspian Sea the stocks are dramatically decreasing. The spawning stock of the Russian sturgeon was estimated by Zhuravleva and Ivanova (1999) to be 45,200 t (2,743,000 fish) in 1976–1980 compared with 7,000 t (355,000 fish) in 1991–1995. The total number of spawners for all sturgeon species in the Caspian Sea was over 3.5 million in 1991 and about 500,000 in 1997 according to Khodorevskaya et al. (1997). In an editor's footnote from this paper it was stated that practically all Russian and stellate sturgeon migrating spawners in 1995 were harvested by poachers below the Volgograd Dam.

Acipenser stellatus (Acipenseridae) stellate sturgeon

Distribution
This diadromous species only lives in the Black, Caspian and Azov Seas from which they migrate into rivers. The Azov and Caspian sea populations result from an ancient reproductive isolation. *A. stellatus* from Ural and Volga were continuously introduced in the Kuban and the Don Rivers from 1961–1986. It became established but showed a slower growth rate (13% less) than the native Azov stocks (Tsvetnenko, 1993).

Identification
A sub-species, *A. stellatus donensii*, was proposed but not recognized. It is sympatric with *A. gueldenstaedtii, A. nudiventris* and *H. huso.*

Habitat and reproductive characteristics
Stellate sturgeon live near the coast at depths from 50–100 m to 300 m in winter, but they can live at depths of 3–15 m in the north of the Caspian Sea. They avoid the turbulent waters of estuaries and feed mostly on worms and crustaceans in the Caspian Sea (Polyaninova and Molodtseva, 1995). Stellate sturgeons migrate long distances in rivers in order to reproduce and still have natural spawning grounds below the Volgograd Dam, where 60% of their historic ground is still accessible (Khodorevskaya et al., 1997). They prefer warmer habitats and spawning occurs at higher temperatures than for other sturgeons in the same river.

Stock status and conservation measures
The stellate sturgeon is still captured in the Black, Caspian and Azov seas, but benefited from stocking of juveniles of other species such as *A. gueldenstaedtii*. The stocks have greatly diminished over the last 20 years with captures declining from 13,700 t in 1977 to 5,600 t in 1989. In the Ural there were 1,328,000 migrating individuals in 1977 but only 377,000 in 1988 with 90,000 spawners (number considered as critical). The stock is very low in the Danube (Bacalbasa-Dobrovici, 1997).

Acipenser persicus (Acipenseridae) Persian sturgeon

Distribution
This species is most common in the Caspian Sea and the Volga, Kura, and Ural rivers, and to a smaller degree in the Terek, Suli and Tamur rivers. A small group of individuals live in the Iranian rivers, Sefid-Rud and Gorgan-chaii.

Identification
Pavlov et al., (1994) recognized 2 sub-species. *A. persicus persicus* in the South Caspian Sea and *A. p. colchicus* (Artyukhin and Zarkua, 1986) in the Black Sea and in the Rioni (also known as *A. persicus colchica* Marti, 1940). *A. p. colchicus* has a longer and slimmer rostrum and migrates to the rivers of Georgia and probably in rivers along the Turkish coast. There are few differences among the populations from the different rivers.

Habitat and reproductive characteristics
The diet changes with age and location. In the Caspian Sea, age-one juveniles feed on gammarids, crabs, herrings, and gobies in the south and mysids and gobies in the north. Fully grown individuals feed on mollusks, crabs and fish (Vlasenko et al., in Holcik, 1989). *A. persicus* prefers warmer waters than *A. gueldenstaedtii. A.p. colchicus* spawns in the mountain rivers of the south where the current is rapid, but the temperature is quite warm 20–22 °C (as in the Rioni).

Stock status and conservation measures
A. persicus is much less abundant than *A. gueldenstaedtii* and is concentrated in Iranian waters where sea fishing is permitted. Fishing was prohibited in USSR waters until 1991. There is some artificial propagation. Abdolhay and Baradaran Tahori (1999) reported 5 hatcheries in Iran and fingerling stocking (around 20 million individuals) mostly of *A. persicus*.

Vulnerable

Polyodon spathula (Polyodontidae) North American paddlefish

Distribution
The paddlefish lives in the large hydrographic system of the Mississippian Basin and contiguous rivers that flow into the Gulf of Mexico. Its presence was reported in the Great Lakes; for example, the Lake Erie before 1903 or in lakes Winnebago and Huron (Hubbs and Lagler, 1958). After the creation of the Sakakawea Lake (S. Dakota) the local population of paddlefish increased greatly and substantial recruitment took-place (Scarnecchia et al., 1996).

Identification
This species lives in freshwater but it has the ability to survive in brackish water and can be found in estuaries. Paddlefish reach a length of 2.5 m and a weight of 100 kg. In the Midwest, maturity is reached at 10 years of age (13–14 kg) for females and 8 years of age (7–9 kg) for males.

Habitat and reproductive characteristics
The diet consists principally of zooplankton, captured when swimming with the mouth open, and occasional aquatic insects and seaweed. However, individual daphnia are efficiently located and captured by young paddlefish via the dynamic process of stochastic resonance (enhancement of the weak, specific daphnia signal by random electric noise from the swarm of daphnia, Russel et al., 1999). Spawning takes place between the end of winter and the beginning of spring, on hard-bottomed river beds or, in the absence of rocky ground, on sandy bottoms at lake edges. During spawning migration, they form shoals near the surface. Spawning is controlled by temperature (10–16 °C) but water flow is the triggering stimulus.

Stock status and conservation measures
The decline in paddlefish populations is due to environmental changes such as the loss of spawning grounds and rearing habitat. Commercial fishing of *P. spathula* has diminished in most of its range, but it continues for certain populations and may increase due to the value of its caviar. Over-exploitation in Alabama and Tennessee led to stock reductions. In Louisiana, accidental capture while fishing for catfish amounts to 12 t year^{-1} and a limited quota for game fishing (one fish day^{-1}) was instituted in 1986 (Reed et al., 1992). The paddlefish is a protected species in Idaho and Texas, and is in decline in 10 other states (their geographic distribution is 22 states). Ten states are stocking paddlefish to supplement existing populations or to recover populations in the periphery of its native range (Graham, 1997). Because of their feeding regime, based on endogenous plankton production in ponds, *P. spathula* was introduced in the Soviet Union in 1974 and it is now present in Russia, Romania and Moldavia as part of polyculture systems that produce meat and caviar from females cultured in ponds or in reservoirs (Cuvinciuc, 1995; Vedrasco et al., 2001). Successful farming is starting in the USA (Mims and Shelton, 1999).

Scaphirhynchus platorynchus (Acipenseridae) shovelnose sturgeon

Distribution
Lives in freshwater in the lower and middle parts of the Mississippi River but had a larger distribution in this basin in the past (Ohio, Illinois, Wabash and Cumberland rivers).

Identification
It is one of the smallest sturgeons in North America, usually weighing less than 2.5 kg. It can get bigger in the upper Missouri River (weighing up to 7 kg). It is found in large turbid rivers in areas of current over sandy bottoms or near rocky places or bars and it often concentrates in areas below dams or at the mouth of tributaries. Population density may be up to 2,500 individuals km^{-1}.

Habitat and reproductive characteristics
It reproduces in the Mississippi. Most males mature at 5 years of age and most females at 7 years of age. Adults do not spawn every year. In part of its range it is sympatric with *S. albus* with which it can hybridize. It mostly eats aquatic insects and other invertebrates, lives on gravel or sandy bottoms where a strong current exists and is more abundant than *S. albus*. Details of the life history and its present status are given by Keenlyne (1997). Maturity occurs after 5 to 7 years of age at 0.5 m for males and 0.63 m for females.

Stock status and conservation measures
It was very abundant early in the 20th century, which created an important commercial fishery that still exists locally; 25 t are captured commercially each

year. There is some interest in their potential as aquarium fish. It is classified as a sport fish in 12 of 24 states where it lives. Protected and in decline in Texas, it has the status of "Special Concern" (Johnson, 1987) in Kentucky, Montana, North Dakota, W. Virginia, and Wyoming. Water and sediment pollution can affect this species and high concentrations of contaminants (selenium, organochlorides) are found in the ovaries and meat (to such a degree that it is not recommended for human consumption). This species needs more measures of protection.

Acipenser brevirostrum (Acipenseridae) shortnose sturgeon

Distribution

This species lives in rivers by the East Atlantic coast of North America, from Florida to New Brunswick in Canada. It is found mostly in fresh or brackish water but occasionally far out to sea (29.5–30‰ salinity) and it maintains a hypo-osmotic blood plasma level (Krayushkina, 1998). *A. brevirostrum* and *A. oxyrinchus* both inhabit the Hudson River, use the same deep channel, feed on the same taxa, but spawn in different sites (Bain, 1997).

Identification

It reaches a length of about 120 cm and 24 kg; maximum recorded size for a female is 1.43 m and 24 kg and for a male is 1.08 m and 9.5 kg. It lives a maximum 50–60 years. The upstream spawning migration pattern in the Merrimak River, was studied by Kieffer and Kynard (1993). They showed that when the distance from the wintering to spawning area is long (> 50 km) most fish migrate in fall and when the distance is short (< 25 km) migration occurs in spring. Fish migrate in spring when the water temperature reaches 7 °C and discharges 570 m^3s^{-1}. When the fish arrive at the spawning grounds the temperature ranges from 8–10 °C.

Habitat and reproductive characteristics

Although landlocked populations are found, shortnose sturgeon is considered to be freshwater amphidromous by Bemis and Kynard (1997). When they reach adult size (46–50 cm) they display migratory behavior, traveling upstream in spring (in large rivers they may overwinter in deep waters adjacent to spawning areas). Juveniles may remain in tidal fresh and brackish water downstream from their native rivers for 2–8 years.

Stock status and conservation measures

A. brevirostrum has been of little commercial value due to its small size yet it is still in decline in 15 states (it also receives protection in 13 states). Capture of this species is prohibited in United States waters. Since the 1970s, the size of the Hudson River population has increased from 30,000 to more than 38,000 and the population of the Connecticut River seems unchanged (Bain, 1997; Kynard, 1997). From detailed studies during the 22 years since the listing of the shortnose sturgeon in 1973, it is possible to make objective predictions of what can be expected from conservation measures. Studies on cultivation and stock enhancement have started in the southern USA and the first results are promising (Smith et al., 1995).

Acipenser fulvescens (Acipenseridae) lake sturgeon

Distribution

This species is found in three major drainages; the Mississippi River, the Great Lakes, and the Hudson Bay. It is gregarious and is usually found in shallow freshwater (some specimens were found in brackish waters in Quebec). It lives in lakes and in calm areas of rivers, which are not too deep (< 4.5 m) with bottoms made of sand, mud or gravel.

Identification

Like other freshwater species, due to isolation and the limited restocking of lake sturgeon, individuals present in a given watershed basin have kept their original genomic characteristics. Ferguson and Duckworth (1997) identified two haplotypes from analysis of mitochondrial DNA variations. Fish from the Great Lakes/St. Lawrence and Mississippi system carried a single haplotype, while populations from the Hudson St. James Bay carried both haplotypes. They suggested that fish from one refugium (Missourian) recolonized the Hudson St. James Bay drainage and those of a second (Mississippian) recolonized the other drainage. Guénette et al. (1993), also using mitochondrial DNA variation, showed relatively low genetic divergence in *A. fulvescens* from the St. Lawrence River and the James Bay drainage basin. Fortin et al. (1991) attributed the status of useable fishing stocks to the diverse sympatric groups of sturgeons of the St. Lawrence River. These stocks are not recognizable phenotypically.

Habitat and reproductive characteristics

The primary diet is benthic macroinvertebrates, especially insect larvae. Lake sturgeon spawn in late spring either in the lake where they live or more frequently, after a short migration, in small streams on the lake basin. Large, adhesive eggs are released on the shallow gravels in streams or rocky shoals of lakes. Lake sturgeon grow very slowly; 4 to 5 years are required to reach a length of 50 cm and a weight of 0.5 kg.

Stock status and conservation measures

In the St. Pierre and St. Louis lakes, 100–200 t are caught every year (Fortin et al., 1991). In spite of great exploitation at the end of the last century and a considerable diminution of stocks, this species is still abundant in certain basins where it is fished even by sport anglers. In other basins, it continues to be rare and threatened. Due to the high quality of its caviar, the risk of overexploitation is high and fishing is therefore forbidden, or strictly controlled, for most of the stocks. It is protected in 12 states and in decline in 6 others. It is not protected in Canada but signs of overfishing are obvious and biologists recommend the closure or restriction of several fisheries. In Winnebago Lake, improvement of the habitat, which consisted of riprapping riverbanks with large rocks in the 1950s, resulted in an increase in the population due to reduction of erosion and the presence of spawning substrate. In the Menominee River the plan is to re-establish the free passage of sturgeon throughout their former range and, as an interim measure, the fishery will be closed completely every other year (Thuemler, 1997).

Acipenser medirostis (Acipenseridae) American green sturgeon

Distribution

Anadromous species, which lives in the North Pacific and moves up North American rivers, from Southern California to Alaska. Stocks of the various river systems may mix together as adult green sturgeons tagged from the Sacramento River have been recovered in Washington waters. The spawning areas are presently located principally in the Sacramento and Klamath Rivers (California) and in the Rogue (Oregon) (Moyle et al., 1994). In the Klamath River, green sturgeons reach an average length of 1 m in 10 years, 1.5 m by age 15 and 2 m by age 25.

Identification

The validity of this species has been questioned but Birstein and Bemis (1997) concluded that *A. medirotris* and *A. mikadoi* are morphologically similar but genetically different. Van Eenennaam et al. (1999) have counted 249 ± 8 chromosomes in *A. medirostris* from the Sacramento River.

Habitat and reproductive characteristics

Little is known about the biology of the green sturgeon. Adults migrate into freshwater in the spring in California waters and in late summer–early fall in the lower Fraser River. During the migration they are found in large deep pools.

Stock status and conservation measures

Little information exits on the fishing of this species. Green sturgeons are harvested in several NW American River systems and there are concerns that stocks are being over exploited in the Klamath River and in the Columbia estuary. Artificial hybridization with *A. baerii* was reported by Kolman and Krylova (1999). No international protection indicated; species classified as vulnerable in Canada.

Acipenser ruthenus (Acipenseridae) sterlet

Distribution

Wide distribution in Eurasia in the rivers emptying into the Azov, Black, Caspian, Baltic, and Arctic seas and also in the Amur River. Linneus (1758) stated that Frederic I, King of Sweden, had it introduced into his country in 1730. It was introduced in the Pechora River from 1928–1950 and a self-reproducing population has been established but the estimated stock (10–12000 fish) does not permit a commercial catch (Zakharov et al., 1998).

Habitat and reproductive characteristics

A freshwater species, the individuals can migrate into the estuaries to feed but generally live in the middle or lower parts of rivers in strong currents on rocky, gravel or sandy bottoms. The sterlets are sedentary and do not migrate very far upstream if the water level is high. Migrations of 322 km have been reported in the Danube (Hensel and Holcik, 1997). In spring, they leave for flooded areas in quest of food and a place where they can reproduce.

Stock status and conservation measures
It is still exploited in the Danube where it benefits from stocking operations in Hungary (Nevicky and Meszaros, 1992). Fishing was prohibited in the former-USSR. Most populations are listed as endangered, except in the Volga River where the population is at low risk (least concern). Attempts were recently made in Russia to re-establish populations in dam reservoirs of the Volga and Kuban Rivers with some commercial catch.

Acipenser baerii (Acipenseridae) Siberian sturgeon

Distribution and identification
This species is widely distributed in all the rivers of Siberia with typical forms in the Baikal Lake and other river systems such as the Ob, Aldan, and Lena rivers (Sokolov et al., 1986). Three sub-species were recognized: *A. b. baerii* (mainly in the Ob River Basin) and *A. b. baicalensis* and *A. b. stenorhynchus* in the East Siberian Rivers basins (Ruban, 1989, 1997). The validity of these sub-species is still questionable for Birstein and Bemis (1997). Ruban (1998) recognized that the status of subspecies was not reached. *A. baerii* is mostly found in freshwater but certain populations can be seen in estuaries. Juveniles (200 g) of the Baikal Lake population are incapable of regulating their osmotic blood pressure when the salinity is raised to 10.5–12‰ (Krayushkina and Moiseyenko, 1977). The diversity of populations and the characteristic of being strictly a freshwater dweller for some of them, particularly in Iakoutie, could be due to geographic isolations imposed by the Quaternary glaciations which confined and isolated groups in different freshwater environments in eastern Siberia (Kuzmin, 1991). *A. baerii* is sympatric with *A. ruthenus* in a few areas.

Stock status and conservation measures
The stocks remained numerous but a decline was observed in spite of efforts to restock in Siberia. A decrease in average individual weight was observed by Solovov (1997) in the upper reaches of the Ob River after the construction of the Novosibirk hydroelectric power station. Certain original populations are threatened, for example in the Baikal Lake and in the Yenisei, where migrating lake-dwellers were overfished and they were included on the Red-list in 1983 (Pavlov et al., 1985). The decline of the reproductive capacity and development of juveniles results from the construction of dams, which diminish and postpone the flow and the height of the water (Votinov and Kasyanov, 1978), and pollution (Ruban and Akimova, 1991; Akimova and Ruban, 1993, 1995). *A. baerii* populations are vulnerable in the main Siberian Rivers and endangered in the Ob River basin; the Lena River sturgeon is vulnerable and the Baikal sturgeon is endangered (on the Red Book data since 1985). *A. baerii* is now commonly farmed in France, Italy and Hungary to produce meat and caviar (Williot et al., 1993; Bronzi et al., 1999).

Acipenser naccarii (Acipenseridae) Adriatic sturgeon

Distribution and identification
This species is mostly a freshwater dweller but occurs near the coast of the Adriatic Sea in the mouth of the rivers at depths ranging from 10 to 40 m on sand or mud bottoms (Tortonese, in Holcik, 1989). Cataldi et al. (1995) showed that 20 month old (1.9 kg) *A. naccarii* can survive in 30‰ salinity (945 mOsmoles kg^{-1}). One specimen, weighing 71 kg was captured in the Piave River in 1996 and two others in the Pô River (F. Ferrari, pers. comm. 1997). Presently, it seems to exist only in the middle and lower parts of the Pô River. Garrido-Ramos et al. (1997) and Hernando et al. (1999) identified *A. naccarii* in the Iberian Peninsula from, respectively, morphometric studies and differences in a satellite-DNA family plus karyotype analysis but this was not accepted by Elvira and Almodovar (1999).

Stock status and conservation measures
Stocks have always been low historically with annual captures of 2–3 t (Rossi et al., 1991). Specimens from the Pô were captured in 1977, brought to maturity in captivity and reproduced in 1988 (Giovannini et al., 1991). The present farm production is a few hundred tons year $^{-1}$ for consumption and 40,000 specimens (2.5 to 90 cm) were released into the wild between 1988 and 1996 (Arlati et al., 1999). Dams, pollution and poaching are threats for this species (Rossi et al., 1991), which was classified "vulnerable" by Lelek (1987).

Low risk

Acipenser oxyrinchus (Acipenseridae) Atlantic sturgeon

Distribution and identification
The Atlantic sturgeon ranges from the Gulf of Mexico to Labrador (Hamilton Inlet). A sub-species (*A.

oxyrinchus de sotoi or Gulf sturgeon) is generally recognized with populations identified in the southern parts of its distribution (from the Mississippi Delta to the Suwanee River in Florida) and a second northern group (*A. oxyrinchus oxyrinchus*) between Hamilton Inlet and the Gulf of the St. Lawrence/Fundy Bay. The evidence for separate species status for *A. sturio* and *A. oxyrinchus* has yet to be established (Vecsei and Peterson, 2000) and another classification is proposed (see under *A. sturio*). This is an anadromous species spending some time in the St. Lawrence River. It is sympatric with *A. brevirostrum* throughout its range and with *A. fulvescens* in the north and in a few sectors of the St. Lawrence River. This species has the ability to make long oceanic migrations, up to 1,450 km.

Habitat and reproductive characteristics

Out at sea the main prey found in their stomachs are polychaeta and isopods (*Politalana concharum*) but sand and organic debris are the major components (26–75%); the percentage of empty stomachs (no organic or inorganic material) was 67% in spring and 44% in autumn (Johnson et al., 1997). Mason and Clugston (1993) observed empty alimentary canals in the fall in *A. o. oxyrinchus* in the Suwannee River. Spawning can take place at low salinity. The juveniles move rapidly towards the coast and live there until they are 4–6 years old, with periodic returns to freshwater. They then migrate to the sea where they live until sexual maturity at 20–30 years of age. Gulf sturgeons move downstream in the Suwannee River at a speed of 6.2 km day^{-1} (Foster and Clugston, 1997). In the mid-Atlantic coastal areas, males mature at 6–10 years and females at 10–20 years.

Stock status and conservation measures

In 1993, 129 metric tons were captured in Canada and 22–24 t in the U.S.A. (Smith and Clugston, 1997). This species is becoming rare. Certain populations are thought to be close to extinction. Serious measures were taken in the recent past with strict management and severe fishing restrictions (Smith, 1985). Fishing was stopped in 1993 in the Hudson River and in some cases a 2.13 mm size limit was established to allow females to spawn at least once. Since 1997, all US fisheries and markets for Atlantic sturgeon are closed until 20 female year classes reach reproductive age. *A. o. de sotoi* is particularly threatened and the complete prohibition of fishing and the encouragement of restocking projects is suggested. The Gulf sturgeon is listed as Vulnerable and the Atlantic sturgeon as Low Risk (near threatened).

Acipenser transmontanus (Acipenseridae) white sturgeon

Distribution and identification

Historically, this species was most common in the Western part of the North American continent, in a zone from California/Mexico to Cook Inlet in Alaska. It is presently confined to California, Oregon and Washington in the United States and to the province of British Columbia. This species is reared in farms for caviar and meat production and, due to accidental release from fish farms, its natural distribution and range may have expanded. For instance, in 1995–1996 white sturgeon escaped from ponds on a private fish hatchery into the Coosa River and may be present in Georgia and Alabama. White sturgeon principally live in fresh and brackish waters but can migrate into the ocean and withstand full salinity once they attain 2–15 kg (McEnroe and Cech, 1985). In general, it stays close to the coast at depths not exceeding 30 m. Certain populations seem to be freshwater dwellers. Growth is slow in the wild: 0.9 m in 8–9 years in the Columbia River.

Habitat and reproductive characteristics

White sturgeon is an opportunist bottom feeder that eats invertebrates and fish. Juveniles feed on mysid shrimp, amphipods or mollusks. Larger specimens eat crustaceans, mollusks and fish such as lamprey, smelt, anchovies and salmonids. Spawning is triggered by high water discharge at velocities between 0.8 to more than 30 m s^{-1}. As a result, the semi-buoyant fertilized eggs drift considerable distances downstream prior to sinking and adhering to the substrate. DeVore et al. (1995) reported that the lower Columbia River white sturgeon population showed higher reproductive performance compared to those of the Sacramento, San Joaquin estuary and the Fraser River. This is due to suitable spring flow for spawning, easy access to the marine environment and abundant food resources.

Stock status and conservation measures

Captures by sport and commercial fisheries have considerably increased in Oregon and in Washington. It continues to be exploited by the sport fishing industry in California (Kohlhorst, 1995). It is protected in Idaho and in Montana. It is now farmed in the USA (Conte et al., 1988), where extensive research has been carried out especially on reproduction (Doroshov et al., 1997). In Europe (Italy), fish farmers produce meat and caviar (Muratori, 1994). Beamesderfer and Farr (1997) proposed a strategy for the protection and the restoration of the white sturgeon in the Columbia River. Lake and river Kootenai populations on the Columbia River, which are naturally landlocked, are Endangered but those of the Pacific coast rivers are listed at Low Risk (near threatened).

Conservation of sturgeon and paddlefish

Reasons for the decline of populations

Overfishing: an historical concern
This review shows that most stocks of sturgeon are declining but the stock status and conservation measures vary greatly among species or populations. Captures of the Azov and Caspian sturgeon, which represent 90% of the world landings, were 24,000–25,000 t annually during the years 1970 to 1985, but are now less than 2,000 t. Stocks will be exterminated within 5–7 years according to Lukyanenko et al. (1999) while Ivanov et al. (1999) stated that the fisheries will be totally closed within one or two years. It is difficult to relate the threatened status of a given sturgeon species to any single parameter or change in the environment. It is known that most of the sturgeons have definitely suffered from overfishing. Sturgeons are relatively easy to catch and over-exploitation is certainly an ancient and persistent phenomenon. A text from Hesseluis (a Hamburg monk) dating from the 17th century showed early inference of over-exploitation and excessive capture of juveniles in the Elba River. In the archeological sites of Ralswiek in Germany (8–12th century) and of Gdansk in Poland (10–13th century) the proportion of sturgeons in the excavations fell from 70% at the start to 12–13% at the end of the occupation of both sites, suggesting a progressive exhaustion of the resource (Debus, 1997).

Present overfishing and accidental by-catch of sturgeons
Overfishing, accidental by-catch of juveniles, and poaching (to satisfy the high demand for sturgeon caviar) remain major problems. It is obvious that most of the highly endangered stocks are located in international waters, either at sea or in rivers. Some multi- or bi-lateral agreements may exist for the management and protection of the stocks but they do not work well and the tendency of nations is to catch all the fish they can. In Eurasia, in the Caspian and Black seas, in the lower Danube or in the Amur River, the state of endangered species is recognized by scientists for most sturgeon populations. Government agencies managing rivers, however, do not take appropriate measures of protection and still allow fishing. Moreover, the nearly extinct *P. hermani* and *P. fedtschenkoi* of the Amu or Syr Darya River in central Asia are not protected at all. These same governments often provide overestimates of the potential for sturgeon capture and caviar production to CITES in efforts to increase their export quota. Collins et al. (2000) recommended, for sturgeons in the Southeastern USA, the establishment of reserves to provide protection from fishing gear that generates substantial sturgeon by-catch, primarily in riverine/estuarine gillnet and estuarine/marine trawl fisheries.

Degradation of habitat
Sturgeon suffer from degradation of their physical environment related to damming or river modification for navigation and subsequent habitat loss including changes in flow regimes. After damming, breeders are concentrated on reduced spawning habitats. Egg density as high as 5,000 m^{-2} were observed for the Russian sturgeon with 60% mortality during embryogenesis. River modification results in loss or changes in macroinvertebrate fauna and eliminates adjacent natural flooding areas. Other anthropogenic impacts, such as degradation of water quality and siltation, negatively influence the development of embryos and reduce the abundance of benthic invertebrates found in the diet of most sturgeons in rivers, estuaries and the sea. Experience in America has shown that restoration efforts that do not address habitat degradation have generally failed to restore healthy sturgeon populations. Accurate information about the habitat used by juveniles and adults in freshwater rivers, lakes, backwater and estuarine areas is required for each stage of the life cycle (migration, foraging, spawning, nursing, overwintering).

Recent improvements in telemetry technologies have been of great value (Kynard et al., 2000). Obstruction by dams is a major problem and fish elevator technology (Pavlov, 1989) is not very effective for sturgeon. Chebanov et al., (1998) reported the passage of only 22 breeders at the Krasnodar dam fish lift on the Kuban River during 1991–1995 (63,000 were predicted). Kynard (1997) recorded only 81 shortnose sturgeon lifted at the Hoyole dam on the Connecticut

River from 1975 to 1995. This level of passage does not contribute much to total reproduction, but does ensure some gene flow within the population above the dam.

Water discharged from reservoirs should meet the needs of spawners. Auer (1996a) showed that water discharge that resembled the natural regime resulted in better reproductive performances of *A. fulvescens* below the dam (more females present and less time spent on the spawning site). Protection of spawning areas is necessary and gravel extraction should be prohibited. Restoration of degraded sites has been attempted with the construction of artificial spawning channels made of stones and gravel below dams where the spawners congregate. One such site was built below the Federowskaya dam on the Kuban River, but it was entirely silted-in within a few years. It was replaced by a new spawning bed, which was constructed near the edge of the river and had the appropriate water flow regime to attract mature spawners (Chebanov, 1998; Chebanov et al., 1998). In the 1980s, 48 ha of spawning beds were established in the Volga with 2–6 cm gravel at depths of 2–6 m (floodable) or 6–12 m (in the river bed). The density of eggs was highly variable: 60 to 4,000 per m^2. Spanning channels with a large variety of substrates and appropriate water velocity have also been developed in the USA (Kynard, 1997).

Contamination of water and sediments by pollutants

Another reason for sturgeon population decline is the alteration of fish physiology, especially in breeders, by "pollution" (i.e., degradation of water quality with toxic substances accumulated in the sediments in rivers and in the sea). Alterations of oogenesis were identified as early as 1964 in some females of *A. baerii* (Lena River population) and affected 77–100% of the females in the Indigirka River by 1987 (Ruban, 1997). Alterations in the ovarian structure of some Azov Sea sturgeons were also reported by Moiseeva et al. (1997). Degradation of water quality and sediments in the Caspian Sea were found to result in muscle atrophy (Khodorevskaya et al., 1997) and hepatotoxicity (Geraskin, 1995) in commercial sturgeons. Since 1978, elevation of the level of the Caspian Sea submerged former industrial zones that contained hydrocarbons and various toxic compounds thus adding additional sources of pollution (Dumont, 1995). This resulted in a 15-fold decline in the recruitment of biomass of plankton and benthos (Ivanov et al., 1999). Sea level variations also affect the juveniles in nursery areas in the North Caspian Sea (Shagaeva et al., 1993). Problems with pollution have been reported in North America (Smith and Clugston, 1997). In the St Lawrence River, the PCB concentrations in the flesh of Atlantic sturgeon exceed the limit of the FDA guidelines for human consumption (2 mg l^{-1}) and in the Hudson River PCBs were found in a range of 0.15–1.70 mg l^{-1} (with 7.92 mg l^{-1} in the sturgeon brain). In samples of beluga caviar from the Black Sea, concentrations of DDT and PCB were respectively 3.6 and 0.4 mg kg^{-1} (wet weight) (Wirth et al., 2000).

A new threat in the Caspian Sea is the invasion of the alien Ctenophore *Mnemiopsis leidyi*, which reduces the availability of zooplankton and consumes eggs and larvae (V. P. Ivanov and G. I. Ruban unpublished data).

Genetic variability and size of populations

Recent work using enzymatic polymorphism and molecular analyses of mitochondrial or nuclear DNA demonstrates the genetic variability of some wild sturgeon populations. In general, the variability is low, with numerous, more or less structured, populations of limited size for most species. A latitudinal cline in genotypic diversity involving at least 7 genetic stocks was found for *A. o. oxyrinchus*. This study documented low diversity in a Canadian population that colonized a glaciated drainage basin to higher diversity in some populations in southern non-glaciated regions (Wirgin et al., 2000).

Molecular systematics has shown separate populations and reproductive isolation of *A.o. de sotoi* in several rivers in the Gulf of Mexico (Wirgin et al., 1997). Levels of overall mtDNA diversity of *A. transmontanus* populations were significantly lower in the Columbia River than in the Frazer River, despite the fact that the Frazer population is younger. This was interpreted as the result of reduced access to the historic spawning sites of the Columbia River due to the construction of dams. This study also suggests that a loss of genetic diversity may occur in a short period of time. Low genetic diversity was also reported in *A. fulvescens* from the St Lawrence River, in *P. spathula* and *Scaphirhynchus* and was interpreted as a consequence of increased negative anthropogenic influences on population abundance (Wirgin et al., 1997). These findings raise the issue of the critical minimum number of males and females required for reproduction (this is most critical in hatcheries, see below). Little is known about sturgeon reproductive behavior during spawning and its efficiency in maintaining genetic variability. It is important to determine the number of males and females involved in spawning and how they participate. Migration by pair (one male and one female) is often reported by fishermen but the number of males that participate in fertilization of the eggs of any given female is not known.

The problem of abundance of adults is important both in terms of the theoretical number of spawners to maintain sufficient genetic variability (low abundance of spawners results in inbreeding depression) and in terms of the biomass of spawners to supply enough gametes to ensure recruitment of the desired level for sustainable catch by commercial or recreational fisheries. The number of spawners is known in some cases. Sulak and Clugston (1999) established that of the 7,650 individual of the *A.o. de sotoi* population in the Suwannee River, 80 females spawn annually. The spawning stock of *A. sinensis* is about 1,000 individuals in the Yangtze River (Q. Wei unpublished data). The weakness of *A. sturio* (critically endangered) compared to the relatively good condition of the closely related *A. o. oxyrinchus* (low risk) may be due to historically higher adult abundance and a larger number of major rivers which can house these species in North America compared to Europe. Bemis and Kynard (1997) listed 17 major rivers between Hamilton Inlet and the St. John's River on the North American continent and less than 10 in the western European coast.

Kynard (1997) found that among 11 surveyed populations of *A. brevirostrum*, five were below or near the minimum viable population level of 1,000 adults suggested for endangered populations. The same author related the number of adults with the length of unobstructed rivers and, more precisely, the migratory distance from the sea to the spawning site (e.g., the Hudson River, 246 km with 38,000 adults and the Merrimack River dammed at km 32 with less than 100 spawners). At long distances from the sea the non-migratory larvae and young-of-the-year stay longer in freshwater (in which predation is more limited) and are not exposed to salt water until osmoregulatory mechanisms are fully developed. The reasons for spawning high up-river are diversely interpreted by authors. Sulak and Clugston (1999) suggest the main reason is the presence of suitable spawning substrate and hydrochemical and hydrological quality needed for gamete fertilization and early development. Auer (1996b) suggests a long swimming distance is necessary for the females to reach full maturity.

Several populations or races are described for many species in the literature. They may be found in the same river system and can be recognized by their migration season or different spawning sites. From a management point of view, it is essential to know if these populations show reproductive isolation, the number of broodstock involved, the extent of gene flow between populations, and the degree of homing fidelity. Technologies such as telemetry are now available for studies that allow the recognition of the spawning time and spawning zones for the shortnose sturgeon (Kynard, 1997). The isolated populations, which exist in fragmented landscapes (for instance those above the Iron Gates Dam on the lower Danube, the Hoyole Dam on the Connecticut River, the Gebouzha Dam on the Yangtze River or in the Kootenai River in the upper Columbia River), should be studied as such and managed as a metapopulation (Hanski, 1998).

A major problem raised by juvenile stocking (see below) is the genetic conservation of donor populations. The precise impact of artificial propagation procedures on genetic variability is not known. What total number of males and females should be used and how many males should be used to fertilize females? In general, it is advisable to collect males and females from the same population, usually from a particular drainage basin, and a minimum of 100 equally contributing fish should be used to prevent breeding fitness depression. Most of the time such large numbers are not available and new approaches are needed. One method is to use genetic screening of individuals (microsatellites) for optimization of hatchery crosses and maximization of gene diversity (Wirgin et al., 1997). Another method is to create a "synthetic strain" for stocking when populations are entirely extirpated from a river system by mixing the broodstock from several populations of a given species in order to increase the variability as attempted for farmed trout (Chevassus, 1990) and white sturgeon (Doroshov and Van Eenennaam, 1999).

Stock enhancement

Enhancement of sturgeon stocks via the release of juveniles is a controversial issue. Although stocking programs to supplement natural reproduction have started or are planned (Saint Pierre, 1999; Kynard et al., 2000), this approach is not a priority in North America where the work is concentrated more on fishing regulation, genetic identification of populations, and habitat restoration. Stocking is mostly practiced in the Ponto-Caspian area (Table 1). Several authors consider that stocking of juveniles contributes significantly to sustained populations. From 1980–1983, 20–40 million Russian sturgeons were released into the Caspian Sea; since this was not sufficient to stabilize the population, the number of juveniles released was increased to 40–60 million each year from 1986–1990. In this case the hatchery propagated fish represented 25–30% of the total catch.

Presently, 29 to 32 million juveniles (1–3 g) are released in the Azov Sea (Chebanov and Savelyeva, 1999) and 67 million in the Caspian Sea including 10 million from Iran (Ivanov et al. 1999). Kokoza (1999) stated that 9 hatcheries are still operating on the Volga, releasing 55–60 million fry of *H. huso, A. gueldenstaedtii* and *A. stellatus*; Barannikova (1995) reported a total release of 75 million juveniles for the 3 species in 1992 compared to 92 million in 1989. Although the success of stocking efforts is difficult to assess and requires marking techniques that are not widely available, population dynamics work showed that in the Volga River the proportion of hatchery propagated beluga in the captures was 9.3% in 1971–1975, 77% in 1981–1985 and 96% in 1991–1995 (Khoderevskaya et al., 1999). The present estimate of annual needs is around 150 million juveniles (Ivanov et al., 1999). Raspopov et al. (1995) consider that the stocking approach is not sufficient and that natural reproduction should be maintained in the Volga. This mainly depends upon the flow rate of the river and the number of spawners reaching the spawning grounds.

The Russian indoor or pond rearing procedures for releasing 1–3 g juveniles of the Ponto-Caspian sturgeons species (mainly *H. huso, A. stellatus, A. gueldenstaedtii*) were based on live food (zooplankton, Oligochaeta, Chironomidae), but it was also possible to rear juveniles of some species on artificial food (*A. transmontanus* and *A. baerii* which are now commonly cultivated). Attempts were made to raise juveniles to larger sizes before their release, 10–15 g Kokoza (1999) and even 100–150 g Artyukhin et al. (1999). Rearing technologies in ponds have been elaborated. *A. stellatus* larvae (1.5 g) stocked in fertilized ponds (2400 individuals ha^{-1}) have reached 20 g in the autumn with a survival rate of 50% (Vasile et al., 1998). Paddlefish were stocked by Mims et al., (1991) with 61,775 larvae ha^{-1} in ponds fertilized by organic matter and inoculated with *Daphnia pulex* and this produced juveniles $>$ 120 mm T L with a survival of 77% after 40 days.

Changes in release technologies have also occurred. In 1992, only 15% of juveniles were transported and released directly onto their feeding grounds in the Caspian Sea compared to 40–50% at the end of the 1970s (Levin, 1995). Now changes in stocking practice are under way. Rearing time in ponds is limited to 15 days, when the fry have consumed most of the available live food and are released into lagoons, with a gradient of salinity (0 to 5‰), and enough benthic and planktonic food supplies. Juveniles are placed in large enclosures (200 m^3) for about one day to adapt to the new environment (after release the young fish stay immobile for a few hours and are very vulnerable to predators). Other parameters, such as climatic and hydrological conditions, are also taken into account when stocking. Juveniles are annually stocked in reservoirs above dams to establish self-reproducing landlocked populations e.g., in the Kuban River (Chebanov, 1998).

Recovery plans and conservation measures

Recovery plans, involving research programs, have been established in North America to restore sturgeon populations (Graham et al., 1995; LaPatra et al., 1999; Duke et al., 1999). A first step is the listing of sturgeon species in Red-books based on a large number of parameters (UICN, 1996). The classification as “Threatened” in the USA prompts the establishment of recovery management plans. Fishery surveys and research were carried out under the U.S. Endangered Species Act. After 20 years these activities resulted in an impressive set of data for most of the North American sturgeon. Reliable knowledge of the biology and ecology of most species and populations was provided based upon the migration, habitat requirements, population dynamics and genetic variability of stocks. Actions were undertaken on habitat restoration, artificial propagation and public education in coordination with national recovery efforts. Presently, most of the species in this area are under successful recovery programs. The overall situation for the North American sturgeon populations is better than for populations elsewhere in the world despite the fact there has been local political and industrial opposition to listing a species due to potential environmental constraints as in the case of the Alabama sturgeon (Mayden and Kuhajda, 1997).

A sturgeon recovery plan must be well designed since it takes 10 to 20 years before its impact can be fully evaluated. Restoration programs require a large variety of information on sturgeon and other aquatic species as well. Therefore, it is of interest to produce and keep up to date extensive reviews of the relevant literature. Interdisciplinary approaches are necessary when setting up a recovery plan for sturgeon and should involve social sciences (jurists, sociologists, historians, geographers etc.) in close cooperation with biologists, river managers, fish culturists, administrators, fishermen, consumer and angler associations. Politicians are also involved as they may have to restrict captures and even decide to close fisheries, which is often the most urgent (and most difficult) decision to make. All parties should be involved in determining ownership of released juveniles and more generally of sturgeons captured when fishing is permitted.

The long term monitoring of wild populations (life history, distribution, abundance and data collection on habitat and populations) as carried out in North America, already exists in central Europe and Russia (see the number of references for each species in Table 1) and represents basic information required for conservation measures. Since most populations are located, for at least part of their life, in international waters, the implementation of recovery plans is very complex.

Sturgeon farming as a complementary conservation measure

Farming technologies are well established in intensive systems for *A. baerii, A. transmontanus* and the bester and in pond culture for *P. spathula, A. stellatus* and *A. gueldenstaedtii*. Aquaculture allows the production of caviar from farmed species (8 t produced in the USA and 7 t in Europe in 2000). Hopefully this activity will reduce fishing pressure. Two production systems are emerging (Figure 4).

Farming systems based on captive broodstocks

The use of domesticated strains, managed according to methodologies established for newly farmed species includes: (1) broodstock collection large enough to ensure sufficient initial genetic variability; (2) broodstock management with regular introduction of new donors or use of the "multiple closed gene pools" approach to minimize inbreeding depression which is common in cases of limited broodfish; and (3) genetic improvements by the various methods of selective breeding (Chevassus, 1990). Some adjustments will be necessary in sturgeon because the interval between generations is long (6–8 years in captivity). In Russia, a good technology for rearing broodstock has never been established on a large scale as breeders are usually taken from the wild. This intensive production system is entirely independent of the wild populations and farmed individuals must not be released into the wild. This is the present situation in France and Italy with the production of caviar from *A. baerii* and *A. transmontanus* respectively (not allowed in open water). A similar system is starting in Russia with beluga, stellate and Russian sturgeon and various hybrids for meat production (Chebanov and Billard, 2001). In central Europe *P. spathula* is a good candidate for farming as it feeds on plankton and could yield caviar.

Combination of farming and stocking

The combination of farming and stock enhancement started in Romania with *A. stellatus* and *A. gueldenstaedtii* and Bulgaria with *H. huso*. The objective is to start farming operations from wild juveniles, submature and mature adults taken from the Danube and reared in hatchery facilities at the Brates experimental fish in Galati (Patriche et al., 1999). Mature males and females captured from the Danube are transported to the experimental station to receive hormone-induced spermiation/ovulation treatment. The larvae are hatched and grown in outdoor fertilized polyculture ponds (with cyprinids) so that the juveniles are exposed to a simulated wild environment. Juveniles and adult sturgeons and paddlefish are also reared in polyculture ponds, which are fertilized organically.

In these extensive systems the growth rate is low, but eventually the fish reach maturity and produce viable eggs. This technology is well adapted to the present situation in central Europe where the polyculture system is well controlled and pelleted feeds are not economically available. In this combined farming and stocking approach, production of caviar is risky and should eventually be discontinued, as the pressure on the wild populations may be too high. As a substitute, a specific caviar production system should be implemented (similar to *A. baerii* or *A. transmon* in the E.U.; Figure 4). In the lower Danube, stocking may be not appropriate as there is no stocking tradition, no data on return rate, and virtually no legal protection. The few juveniles produced may be more appropriately released to a farm to establish captive broodstock for each local population. The resulting broodfish would produce juveniles for meat and caviar produc-

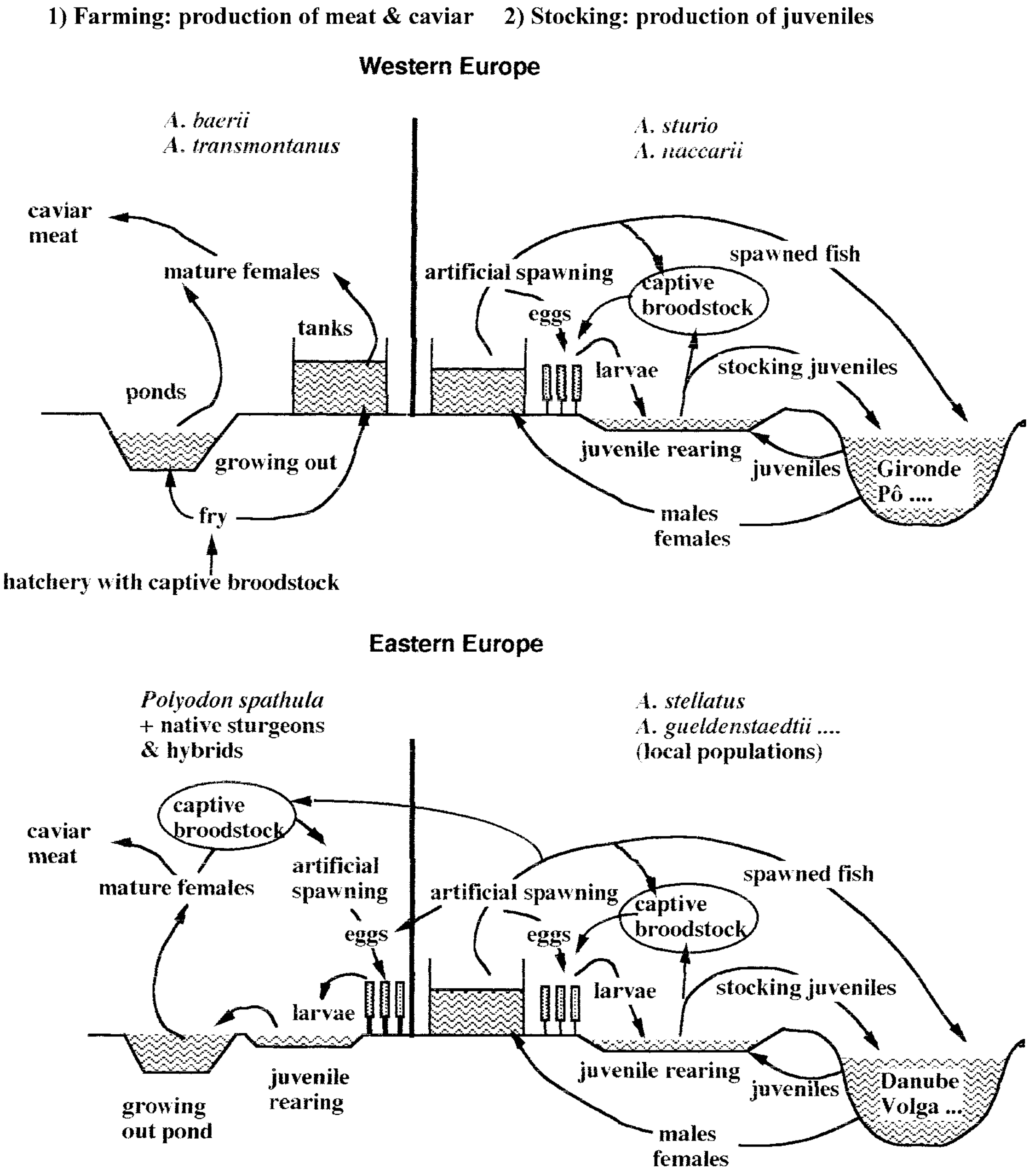

Figure 4. Schematic representation of two systems of sturgeon culture. One (right) is for the production of juveniles of local populations for stocking; males and females are directly taken from the river or grown in captivity. After spawning, spent males and females are released back into river (some may be kept in culture for the establishment of captive broodstock). After a few weeks or months rearing, the juveniles are released into the wild. In Western Europe the number of native species is more restricted than in Eastern Europe. The other system (left) is for the production of sturgeons (local or exotic species and hybrids) for meat and caviar. Production is intensive (tanks-ponds mostly in Western Europe) or extensive (polyculture more common in Eastern Europe). These cultured sturgeons should not escape into the wild.

tion and eventually, when the Danube environment becomes more favorable, for stocking.

Ex situ *conservation and aquaculture biotechnologies*

Ex situ conservation (keeping and reproducing live sturgeon in fish farms as a mean of conservation) is carried out in several countries. Collection of rare and endangered species is established in some places: the Moscow region, the Far East, Krasnodar, and the Federal Genetic Collection of the Black and Azov Seas (Chebanov et al., 1998; Artyukin et al., 1999). Breeders of several sturgeon species are presently reared in fish farms or in experimental facilities in Hungary, France and Germany. Birstein (1993) and Birstein et al. (1997c) recommended immediate breeding of threatened species: *Pseudoscaphirhynchus* sp., *Psephurus gladius*, *A. sturio*, *A. dabryanus* in order to re-introduce them into their natural environment. This requires appropriate captive breeding programs and a thorough knowledge of the genetic diversity of the species, its geographical structure, and historical pattern of gene flow (Vrijenhoek, 1998).

Technologies are needed to support the efficiency of the CITES listing and to provide information on the origin of the products (species, country) such as those proposed by Chen et al. (1995, 1996), Keyvanfar et al. (1987), DeSalle and Birstein (1996) and Birstein et al. (1999). The technology to obtain monosex female populations in *P. spathula* is in progress (Mims and Shelton, 1999) and will improve the economic efficiency of caviar production, but would not prevent the reproduction of individuals accidentally released from fish farms. Hybridization of *P. spathula* with *A. gueldenstaedtii* has been obtained in laboratory conditions (A. Recoubratsky, personal communication, August 2000).

Sturgeon conservation also takes advantage of some aquaculture biotechnologies. The cryoconservation of sturgeon spermatozoa is now possible with limited success (30% fertilization of eggs on average with an excess of spermatozoa). Although this is not sufficient for routine aquaculture operations, it is acceptable for conservation purposes (Tsvetkova et al., 1996). Sturgeon sperm banks are established in Russia: one at Rybnoe near Moscow, (Ananiev, 1998) and one at Krasnodar (Chebanov, 1998). In certain cases, only males still subsist such as in the population of *A. nudiventris* in the Aral Sea and attempts were made to re-establish the population by androgenesis (Grunina et al., 1999). This procedure consists of irradiating the eggs from a closely related species or population in order to suppress the female pronucleus and to fertilize such eggs with the spermatozoa of a surviving *A. nudiventris* male with the re-establishment of diploidy by dispermic fertilization.

Conclusion

Most of the 27 recognized extant species of sturgeons and paddlefish, all characterized by limited adult abundance, are threatened in their entire range of distribution. Two populations are virtually extinct, six species or populations are critically endangered, eight species are listed as endangered, another eight species or subspecies are vulnerable and only two species or populations are at low risk. The scientific community has established the protective status required. Conservation measures fall into three categories: (1) regulation of capture and trade (CITES listing) including the establishment of reserves to prevent by-catch of sturgeon; (2) protection and restoration of essential habitats; and (3) juvenile stocking those take place mostly in North America and the EU. In the rest of Eurasia, where 2/3 of the species are concentrated and usually found in international waters, the status of Endangered Species is recognized but the regulation of captures does not operate (if a total prohibition is declared it will not be respected and poaching will continue) due to sociological and economic problems. Locally, the poor economic situation is a serious limit to habitat restoration. Large scale stocking, which generates a common resource, was acceptable under the regime of the former USSR and still is under the present transition phase, but eventually the question of property rights for fishing sturgeon will be raised (poaching is a likely response). One solution, encouraged by CITES, was the financial support of stocking by the private sector (caviar processing and fisheries companies). This has started in the Lower Danube but also results in increased fishing pressure.

Sturgeon are in danger as patrimonial species and anthropogenic actions will soon accelerate the extinction of several species. As a resource, sturgeon may be compared to Atlantic salmon, with wild stocks yielding only very limited quantities and aquaculture producing significant volumes of meat and caviar in intensive systems (and possibly polyculture systems). In this context, it is urgent that aquaculture takes advantage of existing genetic variability (in populations where the stock of breeders is above a critical level) and initiates captive brood stocks in fish farms or experimental stations. Part of the flux of eggs from wild stocks should go to hatcheries to be fertilized by mixing gametes from the appropriate number of males and females to be reared to full maturity. Thus, at least for a while, there should be more egg quotas for culture and less for caviar.

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