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The green sturgeon and its environment: past, present, and future

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Much new information about the biology of the green sturgeon (*Acipenser medirostris*) was presented during the symposium "The green sturgeon and its environment" at the 39th Annual Meeting of the California-Nevada Chapter of the American Fisheries Society on 19 March 2005, in Sacramento, California. This was the first time authorities from North America, Europe, and Asia had gathered to talk about the biology of this threatened species. Many of the presenters at this conference prepared articles that are included in this issue. Other scientists who attended the symposium were inspired to prepare additional articles containing their own observations about the biology of the species for inclusion in this volume. Thus, this issue contains sixteen original articles on the physiology, movements, population biology, and distribution of the green sturgeon, and provides the most up-to-date description of the biology of this species. Yet, as occurs so often in science, the sweat and toil of research that drives scientists to publish the results of their studies reveals more unanswered questions. We briefly summarize the findings of the authors published in this special issue, and offer some suggestions for future research, particularly in the context of the imperative need to develop effective regulations and actions to enable recovery of the threatened southern distinct population segment (DPS) of green sturgeon inhabiting the Sacramento-San Joaquin watershed and to conserve this species across its range.

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Physiology

The research presented in this volume contributes to our growing knowledge of the physiological adaptations of green sturgeon to the environments that they inhabit, particularly as larvae and early juveniles. These four articles provide valuable insight into the limitations that physical aspects of their surroundings can impose on this species, and predictive information on where this species may be located at different developmental stages[1]. Werner et al. (2007) expand our understanding on the stress response of green sturgeon (Lankford et al. 2003, 2005, Warren et al. 2004) through their study of temperature related heat-shock protein expression in larval green sturgeon. Their study also sought to bridge the gap between cellular stress studies and whole-organism effects, by linking heat-shock expression with developmental abnormalities. They find that in yolk-sac larvae exposed to chronically high temperatures (26°C), heat shock protein expression is greatest, and correlated with spinal deformities. These results corroborate earlier findings of negative effects on embryos of temperatures greater than 20°C (Van Eenennaam et al. 2005) and tolerance of post yolk-sac larvae and early juveniles of temperatures of 24°C (Allen et al. 2006). In small juvenile green sturgeon, Nguyen and Crocker (2007) demonstrate that substrate composition may affect growth rate, in part through modification of behavior. The availability of different habitat types can affect access to food and shelter; this is reflected in increased activity rates and reduced growth rates. For larger juveniles, Allen and Cech (2007) provide predictive information on distribution from studies of iono-regulatory and osmo-regulatory ability and measures of aerobic metabolism in different salinities at increasing age and size. Finally, Kaufman et al. (2007) relate blood oxygen binding characteristics to environmentally relevant temperatures, and make predictions on the aerobic performance ability of this species and the oxygen composition of the habitats it is likely to occupy. In summary, these studies provide valuable information useful for management of green sturgeon and beneficial in linking the anadromous green sturgeon with other chondrostean and teleostean species.

Gaps still remain in our understanding of the environmental physiology of green sturgeon. Although there are many productive avenues of research that could and, perhaps, should be undertaken at some point, we suggest several that would greatly assist the management and recovery of this species. First, very little information is available on the food and nutrient requirements of the different life stages of green sturgeon. Whether this species has nutritional requirements, and how these requirements or food preferences may play a role in fish residence and migration are not known. Second, the role of environmental and internal cues for downstream migration in juveniles is also not well known. An understanding of the factors contributing to their movements (e.g. timing of water releases, photoperiod, hormonal cues, etc.) will greatly aid the management of regulated river systems that green sturgeon occupy. Third, a more thorough knowledge of the factors affecting upstream migration by adult fish is needed. An understanding of the swimming capabilities of adults and the cues that cause them to move upriver (e.g. water temperature, flow preferences, presence of conspecifics, etc.) will be highly beneficial in the conservation of this species. Fourth, studies that further clarify the effects of potential stressors (e.g. toxicants, dissolved oxygen concentrations) and the nature of the stress response, particularly during sensitive early life history and reproductive stages, are needed.

Movements

Critical to our understanding of the biology of green sturgeon is a clear knowledge of their movements on all scales, from daily activity to spawning migrations. Until recently, the only published description of movements came from the work of Erickson et al. (2002) on the Rogue River in Oregon; five of the papers presented here directly address this topic, however, expanding

[1] *A note on life-stage terminology*: The terms used to describe the different life-stages of fish are often imprecise and may vary between fields of study. In this volume we have used the following conventions: *embryo*—period between fertilization and hatch during which the zygote undergoes cleavage; *larva*—period between hatch and the completion of metamorphosis during which the organism is free swimming yet may be reliant on the yolk-sac; *juvenile*—period between metamorphosis and the onset of maturation (puberty) during which the sturgeon resides in fresh and estuarine waters; *subadult*—period between puberty and full maturity, characterized as large juveniles before to the initiation of spawning, during which the fish enter the coastal ocean; *adult*—mature fish.

our knowledge and providing a firm foundation for both management decisions and future research. First, Moser and Lindley (2007) describe the presence of adults of this species in estuaries in the state of Washington. The fish regularly use these areas during the summer months, although they are not believed to spawn in the associated river systems. This phenomenon has been noted in other articles, but this is the first attempt to specifically quantify the timing of this behavior and to describe movements between coastal habitats. Of particular note, the authors record the presence of individuals from both the northern and the federally ''threatened'' southern DPS in the same estuaries. This suggests that fish from both segments co-mingle when they are not spawning—important information for managers trying to conserve and restore the southern population.

Kelly et al. (2007) provide the first fine-scale description of the daily estuarine movements and habitat use of green sturgeon. The authors detail a manual tracking study of sub-adult and adult fish in the San Francisco Bay Estuary, California, and report that, although the fish tended to occupy the shallower parts of the estuary, sturgeon were apparently not limited by the broad range of environmental conditions in the region, making lengthy directional movements across large gradients. Next, Benson et al. (2007) present the results of a three-year study of spawning migration on the Klamath River, California. Their findings agree with those of Erickson et al. (2002) on the Rogue River, and indicate that the species migrates up-river in the spring, and that most of the fish remain in the river after spawning, staying in deep, low-velocity pools before out-migrating with the advent of the first winter storms. Erickson and Webb (2007) expand on the work first reported in Erickson et al. (2002), describing the results of a five-year study on the Rogue River. The authors were able to refine our understanding of the timing of the migration, identify reaches of the river that may be critical to spawning, and estimate the size at which the species becomes mature. Significantly, because of the duration of their study, they were also able to provide the first empirical description of the interval between spawning migrations, revealing that some individuals return after two -years. Last, Brown (2007) describes the only direct evidence of spawning of southern DPS fish in the Sacramento River, describing the capture of a small number of eggs and larvae.

Clearly, our understanding of the movements and behavior of green sturgeon is still in its infancy, yet we are increasingly able to formulate a basic model, based in large part on the papers included in this special issue. As often occurs, this preliminary understanding not only provides guidance for conservation and management, it also makes clear what we do not yet know, and enables us to refine our questions. Adults and sub-adults may have an extended period of residency in the coastal ocean, although they enter estuaries during the summer months. Often these fish are not engaged in spawning migration and the two genetically distinct population segments intermingle. What is the reason for these estuarine periods, and are there specific habitat needs during this time? While not all fish that enter the estuary spawn each year, some do continue up-stream into their natal system. Where precisely are the fish spawning in the rivers, and what are their habitat requirements? Are the behavior or requirements of fish inhabiting the massive San Francisco Estuary/Sacramento River system different from those in the smaller Rogue or Klamath Rivers? Last, where do the juveniles go? This life-phase remains very much a ''black box''. Do the fish pass rapidly downstream, taking up residence in the estuary before entering the ocean, or is there a river phase first? During this rearing period, what habitat is required? It is our hope that ongoing and future studies will shortly provide answers to these and other questions.

Reproduction and population biology

Many articles in this volume note that green sturgeon are well adapted to persisting in changing environments. Their ability to quickly acclimatize to physiological conditions and make long migrations in salt water, while only needing to make occasional forays into unpredictable freshwater environments to spawn, highlights the benefits of a periodic reproductive strategy. Four articles in this volume build on our understanding of this species' population biology and assess effects of risks at distinct stages of the life history. Webb and Erickson (2007) use histological and immunoassay methods to assess the reproductive condition of green sturgeon during the spring and summer in the Rogue River. These methods provide novel approaches to documenting spawning in lieu of the presence of eggs, and non-invasively determining the sex of green sturgeon (but see Vecsei et al. 2003). The authors observe that although post-ovulatory female green sturgeon are most commonly found in the fall on the Rogue River, a significant proportion of females captured at this time in the river are vitellogenic (with mature eggs), and a female in this reproductive state was also found in the river in the spring. This observation suggests that green sturgeon spend portions of their life in rivers without spawning. Although green sturgeon are regarded as completely anadromous, it is likely they are able to find refuge in freshwater and survive there over long periods at different stages of the reproductive process. This emphasizes the importance of documenting more than just the presence of adult fish in reproductive condition to indicate spawning activity in the river. Thus, validation studies similar to that of Brown (2007), which document eggs and juveniles, are necessary to corroborate that spawning does actually occur in association with upstream reaches containing adult holding areas.

The spawning strategy of green sturgeon enables them to successfully persist through periods when unfavorable conditions may preclude successful recruitment; recent changes in freshwater and ocean ecosystems have made them susceptible to environmental pressures, however. Adams et al. (2007) discuss the primary risk factors affecting green sturgeon populations. Anthropogenic effects including loss of spawning habitat, harvest, and entrainment because of water removal all negatively affect the southern DPS and led to the listing of this population under the US Endangered Species Act (NMFS 2006). Although our knowledge of the population biology of green sturgeon is limited, identification of risk factors is critical to adapting management strategies to favor the life history strategies of green sturgeon.

In management of species such as green sturgeon that:

1 have strong year classes;
2 have long reproductive cycles; and
3 have annual recruitment that may only be a fraction of the spawning stock

the objective should be to maintain a spawning stock of appropriate age-structure (King and McFarlane 2003). Recent changes in how the species is managed have been made with the intention of reducing fishing mortality and increasing the number of times adults can spawn. The states of Washington and Oregon have eliminated all by-catch fisheries for green sturgeon and conservation efforts by Klamath River tribes have increased with new limits on the number of green sturgeon that can be harvested by individual fishers (Langness, personal communication; Hillimeier personal communication). Addressing these issues, Heppell (2007) and Beamesderfer et al. (2007) use distinct frameworks based on life history information to model the effects of mortality and changes in the range of sizes facing additional mortality (i.e. slot limits) on the dynamics of the population of green sturgeon. Heppell uses a population-matrix model to demonstrate that the population growth rate is much more sensitive to the mortality of subadults and adults than to that of juveniles. This analysis suggests that reducing the capture of green sturgeon in fisheries will benefit the species slowly, yet with much greater efficiency than methods involving increased egg production or first-year survival. Beamesderfer et al. (2007) uses a life-history table model to demonstrate that a 30–60% increase in mortality in the first three years of the life cycle would be necessary to reduce egg production per recruit to the biological reference points characteristic of overfishing and stock depletion. The total number of adults may be reduced by 90% with only low levels of additional mortality across all ages (approximately 10%), however, and only 2–5% additional mortality across all ages may be significant enough to reduce reproductive potential below that necessary for stock rebuilding. These analyses support the contention that green sturgeon are susceptible to over-fishing and that management efforts should continue to be precautionary and directed at maintaining an appropriate age-structure for the spawning stocks.

The loss of spawning habitat and the entrainment of fertilized eggs and juveniles because of water removal have been identified as primary risks to green sturgeon (Adams et al. 2007). It is not clear what population effect may be associated with the loss of fish to diversions (Moyle and Israel 2005) or if green sturgeon are able to shift habitat use to compensate for lost habitat. Effective management will benefit from the quantification of both the population's response to these threats and the effectiveness of spawning habitat restoration and re-engineering of fish screens to eliminate these risks. Verifying the annual presence of spawning fish and developing indices of egg abundance in freshwater and juvenile and subadults in estuaries can also provide information enabling assessment of whether the appropriate age-structure exists among spawning green sturgeon. This will enable managers to evaluate the sensitivity of the population to spatially and temporally discrete determinants and risks, and to identify potential recruitment failures before they effect the spawning stock.

Distribution

The three articles in this section discuss the distribution of the green sturgeon and its relatives. In their article on the morphology and ecology of six Pacific sturgeons, Artyukhin et al. (2007) argue that the reduction of characteristics from east to west suggests Asian ancestry whereas, in contrast, the possession of fewer derived characteristics is indicative of North American ancestry. The authors also focus our attention on the taxonomic dilemma of the Sakhalin sturgeon (*A. mikadoi*). The species resembles the green sturgeon in its body proportions and fin count but differs in the number of chromosomes, DNA content per cell, and gene sequences. It remains unresolved whether these are the same or different species, but most observations support the latter conclusion.

Shmigirilov et al. (2007) summarize current knowledge of the general biology and life history of three Asian species of sturgeon: Sakhalin, Amur (*A. schrenckii*), and kaluga (*Huso dauricus*). These species live in the Amur River, Sea of Okhotsk, and Sea of Japan. Sakhalin sturgeon, like green sturgeon, are highly migratory, living most of their lives in the ocean and returning to the rivers only to spawn, whereas Amur sturgeon and kaluga are more sedentary and are distributed in refugial freshwater habitats throughout their lifetime. The Amur sturgeon has two distinct color morphs, brown and gray (Krykhtin and Svirskii 1997). These morphs seem to reside in different regions of the river, the brown morph widely dispersed in the lower and middle reaches of the river whereas the gray morph is confined to four fragmented populations. Similarly, there also seem to be two distinct stocks of kaluga. One spawns in the main stem of the river and migrates to the estuary whereas the other resides in the lower and middle reaches of the river and some tributaries.

Gessner et al. (2007) compare the life histories of the green sturgeon and the European Atlantic sturgeon (*A. sturio*). Both species are similar in their wide-ranging migrations, foraging tactics, growth with age, and diverse populations, but differ in the size of their eggs and fecundity. The larger eggs, larger larvae at hatching, and their lack of a swim-up behavior adapts the green sturgeon to rapidly flowing streams whereas the smaller egg size, greater fecundity, and swim-up behavior of the larvae of the European Atlantic sturgeon adapts it for dispersal in the slowly flowing European rivers. The abundance of both species has been reduced both by excessive fishing and reduction of habitat within their watersheds. The negative human impact on Atlantic sturgeon has been greatest. This species was formerly found off the entire coastline of Europe and adults migrated into large rivers such as the Elbe, Rhine, Gironde, Guadalaquivir, Rhone, Po, Rioni, and Yesil Irmak to spawn; now the only spawning population inhabits the Gironde River in northern France. On the basis of morphological, ecological, and geographic criteria European Atlantic sturgeon used to comprise nine to ten distinct stocks; there is little genetic variability in the current stock, indicating the likelihood of inbreeding (Holcik et al. 1989). Similarly, green sturgeon were formerly recorded from the Bering Sea to Ensenada, Mexico (Moyle 2005), reproducing in the Rogue River in Oregon and in the Klamath, Trinity, Sacramento, and San Joaquin rivers in California. Currently only two spawning populations are known—a northern stock spawning in the Rogue and Klamath Rivers and a southern stock spawning in the Sacramento River (Israel et al. 2004).

One must know the discreteness and range of a species to manage it effectively. The dilemma of whether the Sakhalin is a unique species or the same as the green sturgeon remains a contentious topic that must be resolved by conducting further genetic studies. This symposium, with its resulting publications, is the first time authorities from North America, Europe, and Asia have gathered to address this question from several lines of investigation including classical systematics, genetics, and physiology. Molecular studies, similar to those conducted on green sturgeon, should also be performed on the two morphs of the Amur and kaluga species to determine whether they are distinct stocks.

Telemetry can be used both to follow the fish directly (Kelly et al. 2007) as they move within a region and to automatically monitor long-term and large-scale movements as in the studies presented here by Bensen et al. (2007), Erickson and Webb (2007), and Moser and Lindley (2007). These techniques, with egg matts and larval nets (Brown 2007), could be used to corroborate that the morphs do, indeed, inhabit different regions of the Amur River during most of their lifetime, and spawn periodically in geographically separated reaches.

Conclusion

As is evident from the overview of this volume, much has recently been added to our understanding of the biology of green sturgeon. The symposium on "The green sturgeon and its environment" facilitated this result and should spur future collaborative effort on the biology of green sturgeon among the authors of these articles and other interested researchers and managers. Further studies designed to answer some of the questions revealed here are necessary for conservation and sustained management of this threatened species. In the years to come progress in remote-sensing techniques and equipment will enable scientists to learn even more about green sturgeon migrations and exposure to spatially explicit threats. New efforts to monitor and evaluate the determinants of green sturgeon population dynamics can build on the articles presenting empirical and hypothetical models of population viability, and recovery efforts and adaptive management strategies can utilize the predictive information regarding green sturgeon physiology and movements to understand green sturgeon exposure to risks.

This volume contains a broad foundation for understanding the relationship between green sturgeon and their environment. We believe future research on green sturgeon should be guided by the premise that integrative, multidisciplinary efforts are essential for effective management. Although we are cautious about the future of green sturgeon, it is our hope that compilation of this volume will result in continued cooperation and greater communication between agencies, researchers, and the public toward conserving and managing this species.

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