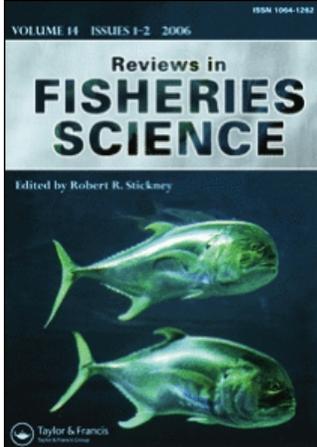


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Sexual Variation in Fisheries Research and Management: When Does Sex Matter?

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In fish, sex determination is a plastic process regulated by a relatively small number of genes that, in turn, leads to a cascade of organism level effects. In other animal taxa, intersexual variation is widespread and has implications in the realms of morphology, behavior, physiology, and bioenergetics. Although relatively well documented in the literature focusing on mammals, birds, and reptiles, the degree to which sex-specific variation is considered is unknown in fish and fisheries research. We examined the scientific literature to evaluate the important sex-related differences in fish and highlighted why some of these differences are of great biological consequence. Sex-specific differences in morphology included sexual size dimorphism, external traits such as coloration, and internal anatomy such as neuron structure. Behavioral differences between the sexes are often linked to reproduction, but there are some documented differences (i.e., variation in aggression and predator avoidance) that are independent of the reproductive period. The potential for sex-related physiological differences are relatively unexplored for fish, although there is strong evidence for disparity in hormone regulation, stress, and immune responses between the sexes. Sex-related variation is also poorly examined in the field of bioenergetics despite the fact that differences in energy requirements and expenditure should and do vary between the sexes. A quantitative literature review of several prominent fisheries journals revealed that sex is often overlooked in fish and fisheries research (between 15 and 44% of articles), which may impair the ability of researchers to detect biologically relevant differences, which in turn can greatly affect management decisions. Although there has been a growing recognition that intra-specific variation (at the population level) is important in fisheries management and research, there is also a need to consider that intersexual diversity exists and is important to understand, conserve, and manage fish and fisheries resources.

Keywords behavior, bioenergetics, intersexual variation, management, morphology, physiology

INTRODUCTION

All variation between the sexes can originally be traced back to the genetic differences resulting from the presence or absence of an assortment of sex-determining genes. In most mammals, sex determination is linked to the presence of the SRY gene, which codes for testis formation and only exists in males (heterogametic individuals with XY sex chromosomes) (Sinclair et al., 1990; Morrish and Sinclair, 2002). Similarly, it has been postulated that bird sex is determined by an assortment of sex-determining genes (the exact mechanism is currently unknown),

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though in these instances females are heterogametic (ZW sex chromosomes) while males are homogametic (ZZ sex chromosomes) (Clinton, 1998; Smith and Sinclair, 2004). The presence or absence of these genes in both mammals and birds leads to differences in gene and, ultimately, protein function during the sex-determining period just days after fertilization of eggs (Morrish and Sinclair, 2002). During this time period, the ultimate sex of an individual is fixed and gonad development occurs (Morrish and Sinclair, 2002). Gonad development, specifically the growth of testis in males, induces a series of hormonal cascades that promote the development of the individual into one sex or the other (Hughes, 2001).

Sex determination in fish is a much more plastic process than sex determination in mammals, birds, and some reptiles, and

this process can significantly differ between species (Shapiro, 1992; Devlin and Nagahama, 2002; Schartl, 2004). In addition to genetic determination, environmental (especially temperature) and hormonal factors may interact to alter sexual development of individual fish (Redding and Patiño, 1993; Devlin and Nagahama, 2002; Schartl, 2004; Ito et al., 2005; Nagahama, 2005; Fujioka, 2006). Genetic determination of sex in fish is a much more complicated system than that of other vertebrates (reviewed in Manolakou et al., 2006). It has been argued that multiple sex determining genes on a host of chromosomes may compete and interact with the environment and hormones to ultimately determine the sex of every individual (Manolakou et al., 2006). Adding to the complexity of the genetic component of sex determination in fish, researchers have postulated that species-specific genes and pathways may exist, thus rendering the concept of a single sex-determining gene conserved across all species defunct (Manolakou et al., 2006). Currently, no sex-determining genes have been described in fish. Differences at the chromosomal level can lead to differences in gene function and production of sex hormones that induce cascading effects, including the formation of male or female gonads. Hormones are then released, which can alter the development of the whole organism and enable it to develop the characteristics of one of the sexes (Yamamoto, 1969; Adkins-Regan, 1987; Devlin and Nagahama, 2002; Piferrer et al., 2005; Strussman and Ito, 2005). Specifically, through studies of the application of sex-determining hormones prior to sex determination in many fish species, it has been revealed that androgen masculinizes embryos while estrogen feminizes individuals, though the roles of these hormones can be reversed (Hunter and Donaldson, 1983; Piferrer and Donaldson, 1991; Kobayashi and Iwamatsu, 2005). Additionally, interactions with environmental factors can affect gene expression and subsequent sex determination (Conover and Fleisher, 1986; Shapiro, 1988). To add to the already complex nature of sex determination in fishes, certain species can be considered truly hermaphroditic and exhibit sex reversal during the adult lifespan (Chan and Yeung, 1983; Shapiro, 1988; Redding and Patiño, 1993; Kroon et al., 2005; Oldfield, 2005; Sato et al., 2005; Nakamura and Kobayashi, 2005).

Once the sex of an individual has been established, gonads play a major role in the formation and release of various sex hormones that can alter nearly every aspect of the biology of the whole organism (Redding and Patiño, 1993). The main functions of sex hormones include the reduction or increase in gonadal tissue (Leatherland et al., 1982; Kobayashi et al., 1988; Barry et al., 1990b), creation of morphological secondary sexual characteristics (Leatherland et al., 1982; Liley and Stacey, 1983; Uglem et al., 2002), and the regulation of spawning behavior (Liley and Stacey, 1983; Barry et al., 1990a; Redding and Patiño, 1993). Additionally, sex hormones have been shown to affect a number of non-reproductive behaviors and processes, ranging from individual enzyme activity to whole organism growth rate and behaviors such as temperature selection (Redding and Patiño, 1993).

In other animal taxa, intersexual variation is widespread and has implications in the realms of morphology, behavior, physiology, and bioenergetics (Shine, 1989). In light of the tremendous variation in sex determination as well as the range of effects of sex differentiation on the whole organism, the goal of this article was to determine the current state of knowledge of intersexual variation in fishes in four key areas (morphology, behavior, physiology, and bioenergetics) and to determine the acknowledgement of possible intersexual variation in current fisheries research. To that end, a literature review was performed to assess the findings of numerous studies in relation to this topic. This qualitative literature review was followed by a quantitative literature review to determine recent trends in the consideration of intersexual variation in fisheries research. Five fisheries journals were surveyed over the last five years of publication for references to intersexual variation in each article to determine the degree to which sex-specific variation is considered in fish and fisheries research.

MATERIALS AND METHODS

Qualitative Literature Review

Between September and November 2006, a qualitative review of the examination or consideration of intersexual variation in fisheries research was performed to determine the current state of knowledge concerning intersexual variation in fishes. Four key areas (morphology, behavior, physiology, and bioenergetics) were identified, and the subsequent literature search was tailored to these areas. During this time period, ISI's Web of Science (1945–present) was searched using the terms presented in Table 1. Results were then screened for relevance before inclusion in the literature review. Studies that did not specifically relate to intersexual variation and one of the key areas were excluded from further synthesis.

Table 1 List of search terms used in Web of Science (1945–present) for the qualitative literature review. Within each area, terms were paired with the word “fish” to filter out results from other taxa. Results were subsequently filtered to remove irrelevant studies

Search term	Number of hits by key area			
	Morphology (morph*)	Behavior (behav*)	Physiology (physio*)	Bioenergetics (bioenerg*)
Sex*	839	1,697	421	16
Sex* specif*	125	0	10	0
Sexes*	153	251	61	2
Intersex* varia*	2	6	1	0
Inter-sex* varia*	0	1	0	0
Sex* bas*	282	357	119	8
Intersex*	33	48	10	0
Inter-sex*	0	6	0	0
Gend* specif*	5	21	6	1
Male*	919	2,089	460	25
Female*	814	1,894	477	21
Total	3,032	6,370	1,589	73

Quantitative Literature Review

In October 2006, a quantitative review of the utilization of intersexual variation in fisheries research was performed. Five years (i.e., January 2001 to December 2005) of five prominent fisheries journals were searched for references to intersexual variation or sex in each article contained therein. The journals were searched to determine if authors mentioned intersexual variation or considered sex as a variable in analysis during the study. These journals were *North American Journal of Fisheries Management (NAJFM)*, *Fisheries Management and Ecology (FME)*, *Transactions of the American Fisheries Society (TAFS)*, *Journal of Fish Biology (JFB)*, and *Canadian Journal of Fisheries and Aquatic Sciences (CJFAS)*. These journals were selected because of our belief that they represent some of the key empirical outlets in the field of fish and fisheries, providing regional coverage in Europe and North America. Though there were only a minor proportion of articles published in these journals, it is important to note that most journals surveyed extend their definition of fish to include invertebrates (e.g., *NAJFM*, *TAFS*) and in some cases include research on plankton, marine mammals, and other aquatic taxa (e.g., *CJFAS*). In addition, some of these journals also publish perspectives (e.g., *CJFAS*) or research on human dimensions (e.g., *NAJFM*, *FME*) for which fish sex is not likely to be relevant. For the purposes of this analysis, we included all peer reviewed articles only and excluded editorials and book reviews. No temporal trends were observed while enumerating studies that included sex as a factor, permitting us to pool data for the 5 years to one set of measures per journal. The proportion of studies that included intersexual variation or sex was considered, and the between-journal comparisons were analyzed by chi-square contingency tables (Zar, 1999). Pairwise comparisons were performed to determine significant differences in a proportion of studies that included intersexual variation or sex in analysis between journals (Zar, 1999).

Qualitative Literature Review

Morphology

In general, morphology is the study of the shape and form of organisms. Perhaps the most obvious instance of sexual dimorphism in fish relates to sex-based coloration of some species. A dramatic example of this is the bright coloration of male guppies (*Halichoeres melanurus*; Kuwamura et al., 2000). Kuwamura et al. (2000) described sexual dimorphism in guppies in terms of body color and fin length. In general, the caudal fin of the male is more vibrant than that of the female and is spotted with black markings. In some hermaphroditic reef species (e.g., parrotfish, *Calotomus* spp.), intersexual variation in coloration exists and can change if an individual changes sexes (Munoz and Warner, 2003). Additionally, many fish species across multiple

families that are normally camouflaged develop conspicuous nuptial coloration during the reproductive period (Cubillos and Guderley, 2000; Standen et al., 2002; Weber and Bannerman, 2004; Casazza et al., 2005; Craig et al., 2005; Gibson and Fries, 2005). These dramatic color differences are related to mate choice, where females tend to prefer brightly colored males (Kuwamura et al., 2000).

Similarly, sexual size dimorphism has been noted in multiple species and is a commonly used indicator of sex. Bullock and Murphy (1994) noted that male yellowmouth grouper (*Mycteroperca interstitialis*) were longer than their female counterparts at the point of maturation, as males take longer to mature than do females. Similarly, Kassam et al. (2004) established that male *Petrotilapia* spp. are larger than their female counterparts. This trend is observed in other species such as chum (*Oncorhynchus keta*) and sockeye (*Oncorhynchus nerka*) salmon, where males (with the exception of precocial males) generally attain a larger size than females by the time of spawning migration (Beacham and Murray, 1985). Conversely, there are also several examples of size dimorphisms where females are larger than conspecific males, such as the boarfish (*Paristiopeterus* spp.) and snipefish (*Macrorhamphosus* spp.; Lopes et al., 2006). In some species, these differences in size and color are due to the development of secondary sexual characteristics related to reproduction, such as changes in body coloration in lake sturgeon (*Acipenser fulvescens*; Craig et al., 2005), dorsal hump formation in Pacific salmonids (*Oncorhynchus* spp.; Quinn and Foote, 1994), and sex-related differences in pectoral fin area in the three-spine stickleback (*Gasterosteus aculeatus*; Hoffmann and Borg, 2006).

The internal anatomy of species may also vary by sex. In particular, killifish (*Fundulus heteroclitus*) have been used to study differences in neuronal morphology, as female killifish have a greater hypothalamic spine density than their male counterparts (Lauer et al., 2006). Sexual dimorphism has also been noted in the dentition of the Atlantic stingray (*Dasyatis Sabina*; Kajiura and Tricas, 1996). Male and female stingray use their teeth differentially, where males use them for mating and feeding, while females use them only for feeding (Kajiura and Tricas, 1996). Consequently, differences have been observed in tooth shape, size, and sharpness (Kajiura and Tricas, 1996). It is during the reproductive period that sex-based differences in internal morphology are especially prevalent. For example, timing of and gamete production can differ between the sexes. For the muskellunge (*Esox masquinongy*), the onset of gametogenesis occurs earlier in females than in males (Lin et al., 1997).

Intersexual differences in the morphology of fish may be considered more frequently by fisheries scientists than the other topics addressed in this article because many differences are external and easily visualized. In particular, sexual dimorphism in size, color, and body structure have been extensively reported in the literature (Table 1). These external differences are critical for sex identification and can be used as tools for research scientists as well as fisheries managers. In addition, these

external differences can translate into differential performance between males and females that have implications for survival and fitness (Hinch and Rand, 1998; Oxenford and Hunte, 1999; Magurran and Garcia, 2000; Standen et al., 2002). Although these morphological differences influence many essential aspects of fish life strategies, they may also have less obvious consequences, such as their influence on diet (Shine, 1991) or habitat use (Weckerly, 1993). In contrast, a very limited number of studies consider internal variation in morphology. Recent work has shown (e.g., Lauer et al., 2006) that these internal differences can be important, having potential implications for individual performance and behavior. Although some aspects of sexual differences in morphology are extensively documented, there remain many opportunities for research on internal sexual differences in the morphology of organs and organ systems.

Behavior

It has long been known that there are individual differences between various animals' behaviors. Behaviors related to feeding, reproduction, and predator avoidance are essential to individual fitness and survival, and differences in the behavior of male and female fish have been well documented (e.g., Davies, 1991; Magurran, 1993; Andersson, 1994). In adult fish, intersexual variation in behavior has been reported for a number of traits including partner preferences (Basolo, 2004; Sneaker, 2006), reproductive behavior (Basolo, 2004), and antipredator responses (Giles and Huntingford, 1984).

During the reproductive period, there is great variation in body size preference between males and females (Basolo, 2004; Santangelo and Itzkowitz, 2004). In many fish species, males preferentially choose to mate with larger females (Downhower and Brown, 1981), and this preference may be largely due to the positive relationship between female body size and fecundity in most ectotherms (Trivers, 1972). For example, in a study of *Brachyrhaphis rhabdophora*, Basolo (2004) found that large males preferentially mated with large females, while small males were relegated to smaller females. Additionally, females of any size generally preferred larger males (Basolo, 2004). These interactions between the sexes have been theorized to influence the evolution of alternative reproductive behaviors (Henson and Warner, 1997).

Operational sex ratios can be influenced by the adult sex ratio (Madsen and Shine, 1993), as well as age at maturation (Bjorklund, 1991), mortality rates (Hairston et al., 1983), and migration patterns (Reynolds et al., 1986). The operational sex ratio of a population can then have dramatic effects on behaviors of individuals within that population. In situations with female-biased sex ratios, more female-female interactions and aggressive events are generally present, which suggests an increased competition for males (Kvarnemo et al., 1995). Additionally, males typically show less competitive behavior when females were more numerous (Kvarnemo et al., 1995). Skewed sex ra-

tios have been predicted to give greater opportunities for mate choice in the less abundant sex (Emlen and Oring, 1977).

The majority of fish species provide no parental care for their young (Gross and Sargent, 1985). Nonetheless, parental care occurs in approximately 20% of bony fish families (Gross and Sargent, 1985). Within these care-giving species, roughly 50% are characterized by male-only care (e.g., Centrarchidae and Cichlidae; Gross, 2005), which has been the subject of much research (e.g., Neff and Gross, 2001; Cooke et al., 2006a). Other forms of parental care (sole-female and biparental) have also evolved in fish and represent 30% and 20% of cases, respectively (Gross, 2005). The mode of parental care that a species practices is related to the costs and benefits of the investment of each sex to parental care and gonad formation, leading to tremendous variation in behavior between the sexes of these species during the reproductive period (Gross and Sargent, 1985; Gross, 2005).

Beyond the frequency of parental care differing between the sexes, other dramatic differences in behavior also exist. In the majority of sunfish (Centrarchidae), males construct nests, court females, and provide sole parental care for offspring, while females depart after egg deposit and resume feeding and other behaviors (Kramer and Smith, 1962). Similarly, male three-spine stickleback provide sole parental care requiring a suite of pre-spawning behaviors, including territory establishment and defense, nest construction, and courtship of females for which there are no analogous behaviors among their female counterparts (Cubillos and Guderly, 2000). In addition, Pacific salmon show sex-specific behaviors on the spawning grounds, where females excavate redds to which males gather for spawning (Dingle, 1996). During this time, males compete for mates through a variety of displays and aggressive behaviors, such as biting and slashing (Dingle, 1996). Females, however, guard the redd and show a much reduced level of aggression to both males and other females (Dingle, 1996). Reproductive behaviors can also vary according to the conditions at spawn. For a mouth-brooding cichlid, the Galilee St. Peter's fish (*Sarotherodon galileus*), male-only, female-only, and biparental care occur in the same population, but the proportion of care given by these groups depends on current conditions such as operational sex ratios as well as the current fitness benefit (e.g., clutch size) (Balshine-Earn and Earn, 1998).

Other groups of fish show sex-related behaviors unrelated to reproduction period, such as intersexual variation in feeding tactics. Temming and Hammer (1994) reported differences in the diurnal feeding rhythm and prey selection of male and female dab (*Limanda limanda*). Although females always had more food in their stomachs than males, males were found to feed more often in the evening, while females consumed their food in the morning (Temming and Hammer, 1994). Similarly, Sano (1993) found that female sandperch (*Tautoglabrus adspersus*) fed three times faster than males. Dolphin fish (*Coryphaena hippurus*) also show sex differences in diet since males are less able to capture fast swimming prey than their female counterparts

(Oxenford and Hunte, 1999). Much of the intersexual variation in feeding behavior is associated with differences in morphology (Magurran and Garcia, 2000).

Sex-specific differences in the behaviors of immature fish have also been noted (Johnsson and Akerman, 1998). In brown trout (*Salmo trutta*), immature males are much more aggressive than their immature female counterparts (Johnsson et al., 2001). It is thought that these differences in aggression result from differences in maturation timing between the sexes (Johnsson et al., 2001). Brown trout males mature earlier than females (Johnsson, 1989), indicating that aggression may be a selected trait to increase feeding and reproductive opportunities (Johnsson et al., 2001). Additionally, immature males also seem to reduce their behavioral response to predation threats earlier than females (Johnsson et al., 2001). In this case, males may be taking more risks in order to forage and prepare for early maturation (Ludwig and Rowe, 1990). These intersexual differences in aggression and boldness may result from divergent development programs for males and females, gradually preparing them for different roles during the reproductive phase of the life cycle (Johnsson et al., 2001). Though some studies have demonstrated differences in behavior between males and females, the topic of intersexual variation in juvenile fishes has been given little attention.

Many aspects of behavioral intersexual variation are well documented. Much work has focused on reproductive behavior, highlighting areas where males and females differ in mate selection, courtship, and parental care. Sexual differences in foraging behavior are also well recognized, showing that males and females can differ in foraging location, effort, and time. Documented intersexual variation in aggressive, anti-predatory, migratory, and schooling behaviors is limited. Although sexes can differ in their levels of aggression (Cole et al., 1980), risk assessment (Quinn and Kinnison, 1999), migratory behavior (Jonsson et al., 1990), and schooling behavior (Magurran, 1990), little work has fully explored these topics. In addition, opportunities exist to examine the costs of these behaviors as well as the influence of changing environments on these behaviors. Most work has examined these questions in adult fish, especially in relation to the reproductive season, while research into the same topics with respect to juvenile and non-reproducing fish is still quite limited.

Physiology

Physiological processes enable animals to regulate their internal environment and may influence many areas of organismal performance and, ultimately, individual fitness through the control of reproductive and survival mechanisms. In some fish species, physiological sex differences become obvious during the reproductive period. Given that gonadotropins (GTH) play an important role in the regulation of gametogenesis and gonadal steroidogenesis in most fish (Nagahama, 1994), Gen et al. (2000) sought to examine the physiological roles of gonadotropins (GTHs) in the red seabream (*Pagrus major*). In teleosts, two distinct GTHs have been shown to exist: GTH-I homologous to

follicle stimulating hormone (FSH) and GTH-II homologous to luteinizing hormone (LH; reviewed by Melamed et al., 1998). By examining the mRNA expression of α GSU, GTH-I β , and GTH-II β subunit genes, Gen et al. (2000) were able to demonstrate significant sex-related differences. The expression of α GSU and I β mRNA levels were significantly lower in females than in males during the reproduction period and for most of the non-reproduction period. Further work (Gen et al., 2003) has demonstrated that the gene itself, GTH-I (FSH equivalent), plays an important role in male, but not female, gametogenesis. Recently, much attention has been given to the sexual dimorphism in aromatase expression (Melo and Ramsdell, 2001; Gonzalez and Piferrer, 2003; Blázquez and Piferrer, 2004; Goto-Kazeto et al., 2004). Aromatase catalyzes the synthesis of estrogen by the aromatization of androgens, and is a widespread enzyme mostly found in the gonads and the brain (Piferrer et al., 2005). Melo and Ramsdell (2001) have shown that medaka (*Oryzias latipes*) exhibit sex-specific brain aromatase activity, having likely consequences on the gonadal-pituitary-hypothalamic (HPG) axis, which undoubtedly affects sex differentiation and the reproductive cycle (Piferrer and Blázquez, 2005).

Similarly, it is only during the reproduction period that sex-related differences in cardiovascular performance have been noted in largemouth bass (*Micropterus salmoides*; Cooke, 2004). This study found that cardiac output and heart rate was 12–15% greater in nesting males than in non-nesting males and females. These cardiovascular differences are important, as they imply differences in the metabolic costs between sexes during this period. For example, this may infer serious costs to reproductive males, such as reduced cardiac scope (i.e., the difference between resting and maximal cardiac activity; Cooke, 2004). Since males of other groups of fish also provide parental care (Gross and Sargent, 1985), it is possible that these species also exhibit similar sex-related cardiovascular differences. In a recent review, Gamperl and Farrell (2004) also highlight the physiological consequences of the cardiac enlargement that occurs in male, but not female salmonids, at the onset of sexual maturation. Only males show a great increase in cardiac stroke volume to support the differentially greater demands placed on performance of male salmon during reproduction (Franklin and Davie, 1992).

Since the reproductive period may also correspond to a stressful period in an individual's life, researchers have examined the sex-related differences in levels of stress hormones during the breeding season. Kubokawa et al. (1999) have shown that female sockeye salmon (*Onchorynchus nerka*) have relatively high cortisol levels at the commencement of spawning migration, and these levels do not change as the reproductive period progresses. In contrast, male sockeye have relatively low cortisol levels at the start of spawning migration and show a gradual increase, reaching female-equivalent highs at the end of spawning. Similar results have also been noted in the laboratory, where pre-spawning females did not respond to confinement stress and conspecific males did (Kubokawa et al., 2001). Taken together, this suggests that female sockeye salmon have reached their

maximum cortisol release before spawning, which may be related to other associated sex-related physiological changes, most notably ovulation (Kubokawa et al., 1999). Furthermore, Caragher et al. (1989) showed that maturing male and female brown trout had different responses to cortisol implants in which females showed plasma cortisol levels of more than double those of males, thereby leading to differential effects such as decreased levels of reproductive hormones and subsequent gonad development. Intersexual variation in the levels and response to stress hormones can have marked effects on the reproductive function and eventual fitness of individuals.

Other work has shown that differences in stress levels between male and female fish are not only limited to the reproduction period. In a recent study, Øverli et al. (2006) reported that juvenile rainbow trout (*Oncorhynchus mykiss*) also show sex-related differences in response to stress. Locomotory performance was positively related to cortisol levels in females but not in males, and females resumed feeding more rapidly than males after periods of stress (Øverli et al., 2006). Taken together, these findings indicated that females moved less during periods of stress and were also the first to resume feeding. Although their results showed no significant differences in the levels of glucocorticoid between sexes, interactions between cortisol and sex-related hormones may be playing a functional role in these responses (Øverli et al., 2006).

Due to the speed with which physiological status can change when perturbed by abiotic stress, multiple studies have focused on the sex-specific physiological responses of fish to environmental contaminants (Aaltonen et al., 2000; Afonso et al., 2003; Klaper et al., 2006). Exposure to methylmercury (MeHg) has been shown to elicit sex-related responses in fish (Klaper et al., 2006). Male fathead minnows (*Pimephales promelas*) respond by an up-regulation of vitellogenin mRNA, while females show the opposite (i.e., down-regulation). Particularly interesting is the sex-related gene expression patterns that occur following exposure to MeHg, which provides evidence that male and female fathead minnows may have different physiological responses to this exposure (Klaper et al., 2006). Other work (i.e., Aaltonen et al., 2000) has reported sex-related differences in the immune responses of roach (*Rutilus rutilus*) following exposure to primary and secondary treated kraft mill effluent (i.e., effluent from pulp and paper mill). Males showed inhibitory responses (i.e., decreases in the number of antibody-secreting cells and in the number of immunoglobulin-secreting cells in the blood), while females showed decreased as well as increased responses (i.e., decrease in the number of antibody-secreting cells and an increase in the number of immunoglobulin-secreting cells in the blood). Differences in stress responses were also noted, such that male cortisol levels increased in both treatments, while female cortisol levels increased only following the secondary treatment, further indicating that roach females immune response differs from males because immune suppression is often associated with high levels of cortisol (reviewed by Wendelaar Bonga, 1997). There is also evidence that male and female zebrafish (*Danio rerio*) respond differently to hypoxia stress (Rees et al., 2001).

Both sexes were acclimatized to non-lethal hypoxic conditions and exposed to normally lethal levels of hypoxia. Acclimatized males did 9 times better than male controls, while acclimatized females only survived 3 times better than control females (Rees et al., 2001).

Finally, a study by Afonso et al. (2003) provides a cautionary tale relating to sex-specific differences. When reporting the stress effects of bleached kraft mill effluent on juvenile chinook salmon (*Oncorhynchus tshawytscha*), differences were unobservable when sexes were pooled together (Afonso et al., 2003). However, males responded quite differently to the effluent than their female counterparts when data was analyzed with sexes separated. Their results either indicate that females increase cortisol levels sooner than males (i.e., female control fish are already exhibiting their stress response since control females have higher cortisol levels than control males), or that the stress response has been muted in females, or finally, that males and female respond differently to stress (Afonso et al., 2003). Had the sexes remained pooled for analysis, the sex-specific differences in cortisol response would have gone unnoticed.

A limited number of studies have explored sex-specific differences in the physiology of various fish species. Research in the fields of stress response, toxicology, endocrinology, and fitness physiology has shown some novel results showing the influences of sex. Sexes can differ in their stress response (Kubokawa et al., 1999; Rees et al., 2001; Afonso et al., 2003; Øverli et al., 2006), as well as in their responses to toxins (Nichols et al., 2001; Klaper et al., 2006; Sellin and Kolok, 2006). These areas of research show that there are many opportunities to examine whether stress response and toxic effects are sex dependent, which may have significant management implications. Other work has begun to explore sex-specific endocrine disruption (Gen et al., 2000; Devlin and Nagahama, 2002), leaving much opportunity to examine sex-specific consequences of this disruption and its influence on circulating hormones. Other topics such as cardiovascular, respiratory, immunology, genomics/proteomic, and osmoregulatory physiology have been examined in only a handful of studies. Simply considering sex as a factor in these types of research activities would be extremely informative.

Bioenergetics and Environmental Relations

Bioenergetics is the energy use by an organism for life processes (Tytler and Calow, 1985), and this often includes energy transfer between biotic and abiotic factors. In general, the topic of intersexual variation in the bioenergetics of fish is not well studied (Table 1). Typically, bioenergetic models and studies do not differentiate between the sexes or tend to focus on only one sex engaging in an activity that the other sex does not perform (Hinch and Collins, 1991; Cooke et al., 2002; Steinhart et al., 2005; Shearer et al., 2006) or focus on interspecific differences (Wahl and Stein, 1991; Trudel et al., 2004). Though limited, some studies have investigated the role of intersexual variation in bioenergetics.

Perhaps the most striking differences in energy use between the sexes occur during the reproductive period. Cooke et al. (2001) examined the nesting behavior of largemouth bass with electromyogram (EMGi) telemetry to compare the levels of muscle activity between the sexes. The release of gametes by the female elicited an EMGi increase of about 40% compared to the resting rate (Cooke et al., 2001). Male EMGi rates showed that pre-spawning activities did not involve much muscular activity but that other behaviors such as nest digging and care of offspring elicited increased energy requirements of approximately 30% (Cooke et al., 2001, 2002). Thus, for largemouth bass and presumably for other fish that differ in their spawning and parental care behaviors, energy requirements differ as a result of the stage of reproduction and the sex-related activities. Similar trends have been noted in the non-parental caregiving of Barents Sea capelin (*Mallotus villosus*; Karamushko and Christiansen, 2002), where oviferous females had higher oxygen consumption rates than post-spawn males with the same mass.

Much work has explored the sex-related differences in energy expenditure by anadromous fish during migration and spawning (Williams and Brett, 1987; Altimiras et al., 1996; Jonsson et al., 1997; Hinch and Rand, 1998; Standen et al., 2002). Altimiras et al. (1996) showed that migrating male Atlantic salmon (*Salmo salar*) had higher heart rates than conspecific females, reflecting the males' higher metabolic rate, activity, and subsequent energy usage. During the spawning migration of Pacific salmonids, sex-specific differences in energy use (i.e., power forward propulsion) have been noted (Hinch and Rand, 1998; Standen et al., 2002). During migration, it was observed that male sockeye regularly transit constricted areas faster than female sockeye salmon at the cost of increased energy utilization when compared to slower moving female sockeye (Hinch and Rand, 1998). Similarly, in constricted reaches of the Fraser River, where flow was increased and hydrological regimes were complex, male pink salmon (*Oncorhynchus gorbuscha*) generally used more energy for swimming than did females (Standen et al., 2002). It has also been shown that, across the same migration distance, male pink salmon use up to 15% more energy for swimming than female salmon (Williams and Brett, 1987).

These differences in energy expenditure during migration may arise for a few reasons. First, males may simply have more energy to spend since females have expended a greater amount of their somatic energy on egg production (Jonsson et al., 1997). Second, males can actually improve their overall fitness (i.e., fertilize more eggs) by arriving to the spawning grounds earlier, while females have a set number of eggs and do not share the same advantage (Trivers, 1972; Gross, 1984). Last, these energetic differences could simply be related to the secondary sexual characteristics of sexually maturing salmon. As discussed in the morphology section, male salmon develop a distinct dorsal hump and kype (Brett, 1965), both of which increase hydrodynamic drag and would increase the energy required for forward propulsion (Standen et al., 2002). Work by Crossin et al. (2004)

provides intraspecific evidence for this argument, showing that long-distance sockeye migrants are morphologically different than short-distance sockeye migrants. Migrants that traveled long distances were smaller and more fusiform than conspecifics that traveled short distances and used significantly less somatic energy per unit traveled (Crossin et al., 2004).

The energy required to generate gonads differs drastically between the sexes, and these may lead to alterations in energy intake for males and females. In female lake whitefish (*Coregonus clupeaformis*) and northern pike (*Esox lucius*), female fish tended to eat 30–40% more food than conspecific males (Trudel et al., 2000). Gonadosomatic index (GSI) was determined to be 5% for males and 15% for females, indicating that females invested more energy in gonad development than did males (Trudel et al., 2000). In addition, metabolic rates in female northern pike and whitefish were higher than those of males (Trudel et al., 2000). Thus, females of these two species have increased their rates of consumption as an alternative to decreasing their metabolic rate in order to divert energy to gonad development (Trudel et al., 2000). Sex-specific differences in energy use have also been noted in fish throughout the rest of the year (Vondracek et al., 1996; Robards et al., 1999). In a study of seasonal trends in energy requirements of the Pacific sand lance (*Ammodytes hexapterus*), Robards et al. (1999) showed that sex-related differences in energy densities were only obvious during the reproduction period, where females had higher energy densities than males. Similarly, total energy density differs between male and female brown trout before and after spawning (Berg et al., 1998). Females have the highest total energy content prior to spawning, while males have the highest total energy content post-spawn (Berg et al., 1998). For these two species, sex-related differences in energy densities are most probably related to differential costs of gamete production. Thus, this trend (i.e., females having higher energy densities than males during the spawning period) may be a more frequent occurrence than is reported in the literature.

Intersexual differences in bioenergetics may account for varying responses to contamination. When raised in the presence of sediments containing trace elements, male and female sheepshead minnow (*Cyprinodon variegates*) are differentially affected by the contamination (Rowe, 2003). Males raised in the presence of contaminants (coal combustion residues) showed a decrease in wet mass, while females responded by a decrease in growth and lipid concentration (Rowe, 2003). This suggests that contamination has effects on female, but not male, energy storage and can possibly influence future reproductive output through constraints put on gonad maturation (Rowe, 2003).

Last, environmental conditions have been noted as having sex-specific effects on fish species. Sexes often show a preference for different temperatures (Swain and Morgan, 2001; Hernandez et al., 2002; Wallman and Bennett, 2006) and also exhibit sex-related differences in habitat use (Price et al., 1991; Greenberg and Giller, 2001; Klemetsen et al., 2003). There is also evidence of more subtle environmental relations such as seen in the rockfish (*Sebastes mystinus*). Although this species

normally exhibit sex-specific food consumption rates, these differences were dissipated in El Niño years (Harvey, 2005), showing that environmental change can affect other aspects of fish biology.

Much research has focused on the intersexual nature of growth and reproductive energetics of fish (e.g., Crossin et al., 2004; Yamamoto, 2004); however, it has yet to be determined whether intersexual variation is present or important in other disciplines such as swimming performance, metabolism, thermal relations, and feeding energetics. Currently, there are many opportunities in these fields to conduct comparative studies between the sexes, especially to determine whether potential sex-based differences in activity and swimming performance in the wild (at times other than during reproductive migrations), metabolic rate, and thermal tolerances/preferences exist. The intersexual variation that may occur with respect to relations to abiotic factors is also poorly understood. Recently, some evidence has come to light that different sexes prefer different temperatures throughout the year or seasonally (Swain and Morgan, 2001; Hernandez et al., 2002) and that sexes differ in their habitat use (Greenberg and Giller, 2001; Klemetsen et al., 2003). This field of research can be especially important when applying possible sex-related differences in temperature preference and habitat selection/identification in relation to global climate change. These types of studies may have implications for conservation and management of endangered as well as economically viable fish species if sexes utilize different temperatures and habitats in the face of changing climatic regimes.

Quantitative Literature Review

Reporting Trends for Research on Intersexual Variation

Differences in the proportion of studies that assessed intersexual variation or “sex” between the five selected journals were noted ($\chi^2 = 168.13$, $df = 4$, $p < 0.05$). Studies from the Journal of Fish Biology considered sex and intersexual variation in methods or analyses more frequently than the other journals (Figure 1). Most studies concerning sexual dimorphism in fish were associated with basic research rather than applied management. Often intersexual variation is studied in a context that is addressed in a research study as opposed to a management study. For example, aims of many research projects are related to assessing the sex-related reproduction costs (e.g., Okuda, 2001) or growth rates (e.g., Henderson et al., 2003). Other research programs examine ornamentations to better understand sexual selection (Magurran and Garcia, 2000). Interestingly, there was a trend in all journals where studies focused solely on females more often than males (Figure 1). In general, this was driven due to the fact that many population models employed by fisheries managers include female fecundity as a modeling variable with no corresponding variable for males (e.g., Fayram et al., 2005). Additionally, many studies that focus on breeding competition and habitat quality only consider females because breeding com-

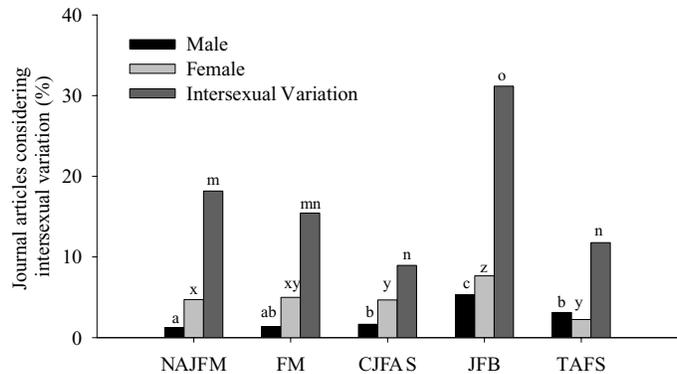


Figure 1 Proportion of total studies in 5 journals (North American Journal of Fisheries Management (NAJFM), Fisheries Management and Ecology (FME), Canadian Journal of Fisheries and Aquatic Sciences (CJFAS), Transactions of the American Fisheries Society (TAFS), and Journal of Fish Biology (JFB)) that considered males, females, or intersexual variation among individuals in methods or analyses during the 5-year period of 2001–2005. Letter assignments (a, b, and c for males; x, y, and z for females; and m, n, and o for sex) denote significantly different ($p < 0.05$) proportions between journals within each sex category based on chi-square pair-wise comparisons.

petition and habitat were assessed only for eggs deposited by the female (e.g., Blanchfield and Ridgway, 2005).

DISCUSSION

Why is Intersexual Variation Studied Primarily During the Reproductive Period?

In almost all aspects of fish research, sex-specific differences are most noted during or related to the reproductive period. Differences in secondary sexual characteristics, behavioral modifications, and associated differences in physiology and bioenergetics have been noted in multiple species during the reproductive period. The focus of research on intersexual variation surrounding reproduction is most likely rooted in the fact that sex-specific differences are most easily observed during reproduction. During the reproductive period, sex-specific differences in some species are readily evident, as males and females display secondary sexual characteristics that make distinguishing the sexes fairly easy to the naked eye (e.g., Standen et al., 2002). Intersexual variation in many aspects of the life of an individual during the reproductive period is rooted in differential costs of reproduction. Due to the fact that eggs are more costly than sperm, and that female fitness is governed by the size and number of eggs produced, production of gametes is generally viewed as the most costly portion of reproduction for females (Trivers, 1972; Gross and Sargent, 1985; Gross, 2005). Contrastingly, male fitness is limited by the number of female mates, making behaviors surrounding reproduction, such as courtship and parental care, the most costly facets of male reproduction (Trivers, 1972; Gross and Sargent, 1985; Gross, 2005). These differences are often reflected in bioenergetic constraints on behavior and physiological variation during reproduction (Trivers, 1972; Gross and Sargent, 1985).

Why Is Intersexual Variation Neglected Year Round?

As a consequence of the focus of research into sex-specific differences during the reproductive period, very few studies focus on these differences throughout the rest of the life history of the fish. The majority of studies in the fields of behavior, bioenergetics, and physiology pool the sexes for analysis of anything unrelated to the reproductive period. This approach relies on the assumption that sexual dimorphisms are not measurable or are not present except during the reproductive period. This assumption may be flawed for a variety of reasons.

Due to the importance of reproduction to all species, as well as the differential costs and trade-offs of reproduction for the sexes, it is quite possible that year-round behavior, physiology, and bioenergetics relate to the reproductive period. As viewed through the growing body of literature on environmental contaminants, the sexes can vary in their responses to contamination irrespective of whether or not they are engaging in reproductive activities (Aaltonen et al., 2000; Afonso et al., 2003; Klaper et al., 2006). These differential responses can be viewed as evidence of marked intersexual variation in physiology and bioenergetics year round. As such, analyses that pool the sexes should be avoided unless initial analyses or a thorough review of the literature provides evidence suggesting that no sex-specific variation occurs in the measurements during that life history or seasonal period. Even then, it may be warranted to conduct exploratory analyses with data to assess whether sex should be considered as an additional factor.

Additionally, various fields of research accept the idea of individual variation as a legitimate source of variation within measurements rather than statistical "noise" (Bennett, 1987; Spicer and Gaston, 1999). Recently, researchers have begun to embrace individual variation in behavior and physiology and develop statistical approaches that explore the role of individual variation on organismal performance and fitness (Kolok, 1992a, 1992b). In general, this variation is attributed partially to differences in development and genetics (Bennett, 1987; Spicer and Gaston, 1999). Due to the different genetics (Shapiro, 1992; Devlin and Nagahama, 2002; Schartl, 2004) as well as developmental processes of males and females (Redding and Patiño, 1993; Devlin and Nagahama, 2002; Ito et al., 2005; Nagahama, 2005; Fujioka, 2006), one can easily see that variation in sex-related traits should occur and be measurable in each of the four fields discussed in this manuscript. As such, studies should take possible intersexual variation into account.

Methods for Determining Sex of Individual Fish

Key to evaluating intersexual variation is the need to easily and reliably identify the sex of fish. Beyond obvious secondary sexual characteristics or other external morphology (e.g., coloration, tubercles), reliably identifying the sex of fish (non-lethally) is a challenge in fisheries research and management. At the most basic level, some species can be accurately sexed based

on external morphology of the urogenital region (Brauhn, 1972; Norton et al., 1976; Noltie, 1985). Multiple species show sex-specific differences in the urogenital region such as the presence of two urogenital pores in channel catfish (Norton et al., 1976), differences in size and appearance of the urogenital pore (Benz and Jacobs, 1986; Noltie, 1985; Vescei et al., 2003), or the presence of external claspers (Moyle and Cech, 2004). Additionally, many species develop secondary sexual characteristics that distinguish the sexes during the spawning period (Brauhn, 1972; Merz and Merz, 2004). Unfortunately, sex-specific dimorphisms are not present in all fish, and juvenile fish that are not sexually mature often do not exhibit the same sex-specific dimorphisms as adult members of the species.

Beyond the presence or absence of morphological differences, several non-invasive methods have been developed to rapidly and efficiently determine the sex of an individual. One such technique that has recently gained popularity is the use of ultrasonography to evaluate the presence or absence of sex organs, which can determine the sex of both mature and immature individuals in many species (Martin-Robichaud and Rommens, 2001). Ultrasonography has been successful in deciphering gonad appearance in mature and immature stellate sturgeon (*Acipenser stellatus*), leading to an accuracy of the ultrasonography sex determination of 97.2% (Moghim et al., 2002). Additionally, acoustic microscopy has been utilized to determine the sex of larval sea lamprey (Maeva et al., 2004). Less technological approaches include palpitation (e.g., for salmonids; Kano, 2005) and the use of blunt probes inserted into the genital pore to differentiate between males and females (e.g., for largemouth bass; Benz and Jacobs, 1986).

As noted above, reproductive hormone titers also vary between sexes. Regressing parameters such as 11 ketotestosterone against estradiol generated two distinct clusters (one male, one female) for sockeye salmon and enabled researchers to non-invasively categorize fish into different sexes during ocean migration when sex cannot be determined from morphology (Cooke et al., 2006b). Heppel and Sullivan (1999) developed a rapid and sensitive biochemical test (enzyme-linked immunosorbent assay) for both sex and maturity of grouper (gag grouper, *Mycteroperca microlepis*; Nassau grouper, *Epinephelus striatus*, and red hind, *Epinephelus guttatus*) based on detection of a sex-specific blood protein (i.e., vitellogenin). For juvenile fish, the aceto-carmin squash technique is useful for differentiating between sexes; however, it requires lethal sampling (Guerrero and Shelton, 1974).

Obviously, not all of these techniques will work on all species and substantial calibration is still needed. Nonetheless, these tools enable the enumeration of male and female fish captured for research and monitoring to be released without terminal sampling, thus reducing unnecessary sampling mortality simply to determine sex and maturity. There is need for additional research on this topic to enable recreational anglers, commercial fishers, and fisheries practitioners (with varied training) to easily and inexpensively assess sex in the field with reasonable certainty.

Management Implications of Ignoring Sexual Variation

For years, sex was a common measurement used in fisheries science and subsequent fisheries management (Larkin, 1978). For example, fisheries managers have long accepted the fact that sex ratio is a key metric in proper management techniques (Larkin, 1978). One of the biggest challenges in managing commercial fisheries is uncertainty regarding sex ratio and reproductive condition as most fish are eviscerated at sea prior to landing to maintain flesh quality and to maximize on-board storage capacity. Stock assessments require knowledge of the proportions of reproductively mature fish of each sex so that estimates of fecundity can be generated. This becomes especially apparent when managing stocks of species that display sequential hermaphroditism. Without basic information on sex of captured fish, as well as the mechanisms and scheduling of sex change, effective management is simply not possible. For example, management actions such as size limits may have unintended consequences on sex-changing species. Most exploited grouper populations, even those with low fishing effort, are female biased (Sadovy and Colin, 1995), which likely influences mating behavior. Due to the sequential hermaphroditism, fishing actively selects for the larger, older, and aggressive fish that typically are male (Coleman et al., 1996), thus exerting selection pressure on sexually mature females to become functional males.

Ignoring intersexual variation can have marked impacts on management schemes and can lead to inadvertent overfishing and population losses of even the most fecund fishes (Sadovy, 2001; Rowe and Hutchings, 2003). Morphological differences between the sexes can cause differential susceptibility of the sexes to capture and harvest both commercial and recreational environmental modification. Size-based differences alone can influence the targeting of one sex over the other for harvest or recreational angling (Coleman et al., 1996; DeMartini et al., 2000). Additionally, timing of commercial and recreational fishery operations can unintentionally target one sex disproportionately with the possibility of altering operating sex ratios (DeMartini et al., 2000; Niemela et al., 2000). Fishing spawning aggregations may alter a number of life history characteristics through decreasing the size of the reproductive population, altering sex ratios, and reducing recruitment, consequently lowering future productivity (Coleman et al., 2000; Rowe and Hutchings, 2003). Indeed, Rowe and Hutchings (2003) noted that proper information on breeding behavior of the sexes in commercially valuable marine species was much more complex than originally known, and ignoring this complexity could be implicated in the collapse of some of these fish stocks.

Typical management strategies include stock enhancement, habitat manipulation or rehabilitation, and development of regulations to conserve fisheries (Cowx and Gerdeaux, 2004). Due to the differential bioenergetics and physiology of the sexes surrounding reproduction, harvest may have uneven sub-lethal effects on the sexes. It has long been known that stress such as angling or commercial bycatch can have deleterious effects on fish reproductive behavior (Pottinger, 1999; Schreck et al.,

2001). Multiple studies have documented sex-specific effects of stress on reproductive behavior, such as delay in ovulation, reduction in gamete quality (both egg and sperm), and subsequent reduced survival of progeny (Campbell et al., 1992, 1994; Contreras-Sanchez et al., 1998). Findings such as these have grave implications for fisheries managers trying to maximize recruitment and bolster recruitment. Differential responses of sexes to common stress warrants the implementation of fisheries management plans that consider intersexual variation as an important facet of modern conservation. Indeed, aquatic protected areas have been proposed as being particularly cognizant of intersexual differences, as they theoretically should protect both sexes (Roberts and Polunin, 1991). However, if the spatial ecology of sexes varies, then it is possible that some protected areas will not function as intended.

CONCLUSION

Many opportunities exist for incorporating sex differences to the overall design of projects as well as analysis and interpretation, especially on the topics of physiology, bioenergetics, and environmental relations. Even basic fisheries assessment programs should be standardized to include "sex" as a metric that is recorded (Bonar and Hubert, 2002). This would enhance the utility of other metrics such as condition factor, which can vary by sex (Cone, 1989). With an increasing focus on intersexual variation in fisheries research, fisheries managers need to recognize the fact that this variation needs to be integrated in management plans. Simply ignoring intersexual variation can lead to poorly informed management plans. There is also growing recognition that life history is intimately linked to physiology and energetics (Young et al., 2006). Core to this "nexus" is the need to assess life history and physiology links on a sex-specific basis. Although there is growing interest in ecosystem management (Link, 2002), this approach needs to be coupled with growing recognition that there is immense individual variation. Recognizing sex-based differences can only enhance management and conservation of global fisheries.

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