

## Integrating physiology and life history to improve fisheries management and conservation

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### Abstract

Knowledge of life-history traits is increasingly recognized as an important criterion for effective management and conservation. Understanding the link between physiology and life history is an important component of this knowledge and in our view is particularly relevant to understanding marine and freshwater fishes. Such linkages (i.e. the life-history/physiology nexus) have been recently advocated for avian systems and here we explore this concept for fish. This paper highlights the gap in fisheries literature with regard to understanding the relationship between physiology and life history, and proposes ways in which this integration could improve fisheries management and conservation. We use three case studies on different fishes (i.e. the Pacific salmon, the grouper complex and tuna) to explore these issues. The physiological structure and function of fish plays a central role in determining stock response to exploitation and changes in the environment. Physiological measures can provide simple indicators necessary for cost-effective monitoring in the evaluation of fisheries sustainability. The declining state of world fisheries and the need to develop and implement restoration strategies, such as hatchery production or protected areas, provides strong incentive to better understand the influence of physiology on population and reproductive dynamics and early life history. Physiology influences key population-level processes, particularly those dealing with reproduction, which must be incorporated into the design and successful implementation of specific and broadscale initiatives (e.g. aquatic protected areas and bycatch reduction). Suggestions are made for how to encourage wider application of the physiology/life-history link, in fisheries management and conservation, as well as more broadly in education and research.

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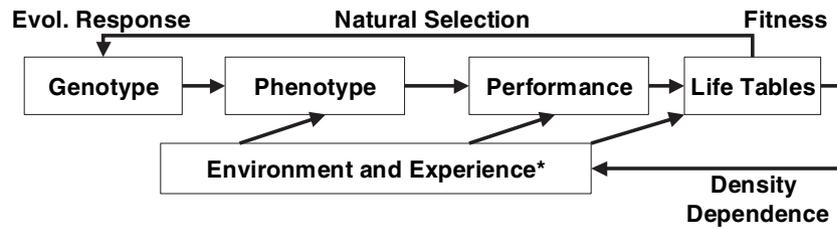
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## Introduction

Life history and phenotypic adaptations to natural and anthropogenic stressors have been studied in fish systems for many years (Alm 1959; Adams 1980; Thorpe 1990; Winemiller and Rose 1992; McCann and Shuter 1997; Jennings *et al.* 1998; Johannes 1998; Pope *et al.* 2000; Rochet 2000; King and McFarlane 2003; Klements *et al.* 2003). The range of life-history traits observed among different species is generally understood as a reflection of their phenotypic responses to environmental conditions (e.g. food availability, predation levels and habitat), to optimize resource allocation over time. Recent advances towards an integrated ecosystem approach to conservation and management have included organismal physiological adaptation as an important link in understanding the relationship between individual- and population-level plasticity (Walsh *et al.* 1998; Rochet 2000; Ricklefs and Wikelski 2002).

Ricklefs and Wikelski (2002) introduced the concept of the ‘physiology/life-history nexus,’ wherein physiology is the key response mechanism

linking both organism and population to their environment. Fig. 1 is modified from Ricklefs and Wikelski (2002) and illustrates the interaction between the environment and the phenotype, performance and life history of an individual. Physiological responses refer to changes in the interlinked systems of an organism, including the cardiorespiratory, endocrine, nervous, immune, gastro-intestinal and musculoskeletal systems. Using examples from endocrine stress responses in birds, Ricklefs and Wikelski (2002) illustrate how physiological sensitivity to the environment can both drive and constrain life-history variation. While constraint is generally understood to arise from the allocation of energy and resources, Ricklefs and Wikelski (2002) suggest that constraint can also arise from control mechanisms that permit only certain combinations of physiology, anatomy and behaviour to occur together. Such physiological states are associated with different life stages of an organism, but also can be triggered by environmental pressures. Ricklefs and Wikelski (2002) show that endocrine-controlled corticosterone levels can alter the behaviour of birds, leading to changes in growth,



**Figure 1** The life history of an individual is derived from genetic information and the environment. The environment progressively influences life history in the expression of phenotype, performance and reproductive success. Life history feeds back to the genotype through the process of natural selection. The organism and population also provides a feedback to the environment through density dependence. The response of an individual, in phenotype, performance and life history, is highly dependent on physiological processes. Modified from Ricklefs and Wikelski (2002). \*Experience explicitly includes exposure of an individual to human-induced impacts, such as air exposure as bycatch or during catch-and-release angling, and the combination life events experienced by an individual (e.g. number of reproductive events and migratory distances).

territory defence and predation risk. New perspectives on the relationship between physiology and life history, and more broadly, on the important role that physiology may play in evolutionary and ecological processes (Chown *et al.* 2004) subsequently have been generated in studies on insects (Chown *et al.* 2003), on plants (Gutschick and BassiriRad 2003), and more generally on organismal design (Piersma and Drent 2003).

Birds were used as a model system by Ricklefs and Wikelski (2002) because of the vast knowledge base that already exists on avian reproductive success and adult survival over latitudinal gradients. However, the fundamental concepts introduced in the physiology/life-history nexus could further enhance our understanding of other systems, in particular aquatic ecosystems. For many reasons, fish can serve as ideal models for further exploring complex linkages between life history and physiology. From a biological perspective, fish are known to exhibit large intraspecific life-history variation (Alm 1959; Adams 1980; Thorpe 1990; Beverton 1992; Winemiller and Rose 1992; McCann and Shuter 1997; Rochet 2000; King and McFarlane 2003; Klementsen *et al.* 2003). Classification of life-history strategies exhibited by fish has varied among studies, but is believed to extend well beyond the traditional *r* and *K* continuum developed for terrestrial animals. In fact, three to five life-history strategies have been proposed for fishes: opportunistic, periodic, equilibrium, salmonic and intermediate (Winemiller and Rose 1992; McCann and Shuter 1997; King and McFarlane 2003). Fish also display a high degree of phenotypic plasticity relative to other animal taxa (Klementsen *et al.* 2003). From a logistical perspective, fish research has been facilitated by their

relatively easy access, breeding characteristics and ability to control for laboratory studies (as compared to birds). These attributes have led to a large base of information in both life history and physiology. Finally, fish are important to humans in terms of a protein source, economics and social/cultural value (Burger 2002; FAO 2002; Ormerod 2003). The preceding reasons support the use of fish as a model system for further exploring the physiology/life-history nexus.

While both life history and physiology of freshwater and marine fishes have been studied individually, little attention has been paid to the link between them and to potential implications for fisheries conservation and management. One notable exception is the early work of Beverton and Holt (1959) which emphasized the relationship between the longevity and mortality rates relative to organismal physiology (and hence the utility of physiological information for determining mortality, or *M*). Unfortunately, those ideas were not fully embraced by managers and conservationists and today physiological approaches are still rarely utilized. Given the current declining state of world fisheries, there is strong incentive to increase understanding of the influence physiology has on population and reproductive dynamics. The combined factors of overfishing, single-species management and delayed response to environmental signals have led to the undisputed decline of marine (Ludwig *et al.* 1993; Pauly *et al.* 2002) and freshwater (Cowx 2002; Allan *et al.* 2005) fisheries. Recent estimates suggest that 47% of the world's fish stocks are already exploited to their maximum sustainable limits, 18% are overexploited and a further 10% are depleted (FAO 2002; Pauly *et al.*

2003). Current issues such as pollution, migration barriers, climate change and habitat destruction have increased the immediate need for conservation of our aquatic ecosystems and the fisheries they support. This need is particularly dire given that less than 0.1% of the global oceans are currently protected, even though they represent 90% of the biosphere (Myers and Worm 2003). In addition, freshwater fishes may be the most threatened group of vertebrates on the Earth after amphibians (Bruton 1995). Regardless of the current state of aquatic ecosystems, there has been negligible emphasis on aquatic issues in the conservation biology literature, and conservation receives limited attention in the general marine, freshwater and fisheries literature (Irish and Norse 1996; Kochin and Levin 2003; Ormerod 2003; Levin and Kochin 2004). The present paper will attempt to address this gap, and illustrate how knowledge of physiology and its integration with life history can provide insight to biologists, conservation scientists and fisheries managers alike. We will focus our attention on three groups of exploited fishes that are heavily managed, exhibit different life-history strategies and occupy different habitats; i.e. Pacific salmon, grouper and tuna. Case studies focused on these three groups of fishes provide diverse coverage of important areas in fisheries research and management. Significant research efforts have been directed towards managing commercial fisheries with relatively abundant studies of physiology and life history, particularly on economically valuable species. However, we contend that the integration of physiology and life history is lacking and the importance of physiology in determining individual and population responses to the environment requires further attention to better manage and conserve fisheries. Although our case studies focus primarily on the marine environment, these issues and the framework we develop are applicable to other fish and other environments.

### Approach

Our efforts focused primarily on literature searches coupled with synthesis and interpretation. This was accomplished using commercial academic search engines that covered primarily peer-reviewed scientific literature (e.g. Fish and Fisheries Worldwide, and Aquatic Sciences and Fisheries Abstracts). We also conducted more inclusive searches using public domain search engines (e.g. Google) in an attempt

to locate forthcoming or more applied examples. In the end, we determined that we required more information from fisheries managers that are associated with the day-to-day management of the three groups of fish that we targeted. To accomplish this, we developed a general survey that was distributed via directed e-mail contact to provincial, state, federal, multijurisdictional and international organizations responsible for the management of specific fishes. The survey was not intended to be quantitative, but instead to supplement our academic literature search with more applied and current management insight. We integrate those general ideas obtained from our informal surveys into our manuscript. While developing case studies, we used the following questions to help provide focus: What is (are) the key management and conservation issue(s)? Has physiology been used? If yes – what physiology and exactly how (or how not) has it helped? If no – what could be done – how could it potentially help? When is physiology not helpful? We use this general framework for all of the case studies presented.

### Case study – the Pacific salmonids

#### Background on Pacific salmonids

Pacific salmon fisheries are an integral component of local and regional economies throughout the northern Pacific Rim. Homing and spawning site fidelity of Pacific salmon species contributes to a wide distribution of genetically distinct populations (Dittman and Quinn 1996; Hilborn *et al.* 2003; Ramstad *et al.* 2003). The life-history traits and phenotypes of these populations exhibit differences in the degree of anadromy, habitat use, difficulty of migration and optimal timing of reproduction. Anadromy, marine navigation, homing and challenging reproductive migrations are dependent on specialized physiological capabilities of salmon, including osmoregulation in fresh- and sea-water, magnetic sense, odour imprinting and homing to natal streams, endocrine-mediated development and maturation, and significant physical endurance (See Hinch *et al.* 2005).

The specialized physiological capabilities of salmon have long been recognized as integral to their distribution and abundance. Although research efforts have focused on understanding the physiology of Pacific salmon, fisheries managers can refine and improve their ability to measure and predict key

management variables, such as recruitment and abundance, through selective incorporation of physiological measures and knowledge. Current research continues to reveal the unique physiological capabilities of salmon and the need for further research to achieve a functional understanding of the response of salmon populations to environmental change and fisheries exploitation.

## Physiology and management

### Management issue: migration energetics, timing and temperature

The management of commercial Pacific salmon fisheries requires the ability to assess the abundance, escapement and spawning success of migratory adults. Capture occurs primarily in the marine and estuary environments on shoals that usually contain multiple stocks and often different Pacific salmon species. To manage for adequate and optimal escapement managers must be able to determine the abundance of migrating salmon, the number of salmon caught in fisheries and the proportion of escaped individuals that will be successful in reaching spawning grounds. A particular challenge for managers is predicting the rate of natural mortality during the nearshore marine and freshwater migration. Research evaluating the role of migration timing, energetics and temperature has further revealed the complexity of predicting en route mortality (Cooke *et al.* 2006; Young *et al.* 2006), but has assisted in managing for this loss and adjusting escapement targets based on factors such as migration timing and freshwater temperature.

Recent studies evaluating the importance of Pacific salmon bioenergetics reveal the integral role of physiology in determining life-history traits and overall fisheries productivity. Upstream spawning migrations of many Pacific salmon stocks are energetically challenging (Crossin *et al.* 2003; Hinch *et al.* 2005). Energy must be efficiently utilized to ensure successful migration, reproductive development (e.g. eggs and secondary sexual traits) and mating, particularly because salmon do not feed during their spawning migration (Brett 1995; Hendry and Berg 1999). The recruitment of juveniles is dependent on the success of this reproductive effort, contributing to the maintenance and productivity of exploited stocks. Studies evaluating metabolic partitioning of resources (Hendry and Berg 1999; Koseki and Maekawa 2002), swimming

performance (Brett 1964; Jain *et al.* 1998; Farrell *et al.* 2003) and bioenergetics models (Hinch *et al.* 2002) of Pacific salmon have provided insights into this potentially limiting life-history stage and improved the ability to predict escapement and recruitment of juveniles to the fishery. In addition to improving the prediction of escapement and recruitment, understanding of the physiology, behaviour and bioenergetics of this life-history stage aids in determining methods for protecting migratory habitat and ensuring suitable conditions during periods when migration occurs. Fish passage at dams or other locations of migratory challenge can be more effectively designed and managed to minimize en route mortality (Hinch and Bratty 2000). Physiological evaluation of body condition and energetic status of migratory salmon can be used to further assist in estimations of en route mortality and adjust escapement targets and exploitation rates accordingly (Cooke *et al.* 2006; Young *et al.* 2006).

Related to migration energetics and presenting a recent and significant concern to managers of the Fraser River salmon fisheries is the effect of freshwater temperature on the migration success of salmon, particularly sockeye (*Oncorhynchus nerka*). Perhaps as a result of climate change, the incidence of unusually high temperature years has increased in the Fraser River. During these years the incidence of en route mortality has increased. Evaluation of the effects of temperature on the aerobic capacity and swimming ability of Chinook (*Oncorhynchus tshawytscha*) and sockeye salmon revealed important stock-specific and overall impacts of temperature on migrating salmon (Lee *et al.* 2003a,b). Routine metabolic rate increased similarly with temperature for different stocks of salmon, indicating the important role temperature plays on metabolism. Stock-specific differences in the response to temperature of maximum oxygen consumption reveal how stocks with differing natal stream temperatures and migration distances have evolved different metabolic capacities. As a result, different stocks are affected differently by temperature and increased temperature beyond the stock-specific optima results in reduced metabolic capacity, increased migration challenge and associated en route mortality. Other controlled studies have further revealed the importance of temperature in maximum aerobic and cardiac scope, indicating a distinct temperature optima and a rapid decline at increased temperatures (Farrell

2002). Farrell (2002) suggests that this rapid decline is related to a decline in cardiac scope associated with a lack of oxygen supply to the tissues. For salmon encountering abnormally high temperatures, this rapid decline in aerobic scope could significantly affect migration success. Increased migration challenge associated with temperature and the occurrence of high en route mortality in extreme temperature years suggests that temperature is likely contributing to en route mortality. The physiological research discussed reveals the importance of temperature and the need to manage escapement conservatively and to account for temperature as a mortality factor in high temperature years. In addition, disease is often mediated by water temperatures and can interact to affect salmonid swimming performance and survival (Wagner *et al.* 2005). Stock-specific thermal optima provide a clear link between life-history traits, performance and the environment.

#### **Management issue: bycatch recovery and post-release survival**

Most fisheries, both commercial and recreational, capture non-target organisms. Many of these bycatch organisms may be economically important and/or their removal presents a conservation concern. In recent years, bycatch of coho salmon (*Oncorhynchus kisutch*) in Fraser River Pacific sockeye salmon fisheries in British Columbia has become a significant conservation concern because of the decline of regional coho salmon populations. As a result, the release of bycatch coho has recently been required (Farrell *et al.* 2001a). However, concerns associated with post-release survival were raised.

Measurement of physiological condition, including levels of muscle lactate and phosphocreatine, revealed that coho salmon caught in commercial troll fisheries were exhausted and stressed immediately after capture (Farrell *et al.* 2001a). However, if captured coho were held in cages alongside the fishing vessel and allowed to swim freely, physiological recovery was rapid. Released individuals displayed no post-capture delayed mortality during a 24-h monitoring period. This research was used to develop and evaluate a fish recovery method to assist with post-capture and release survival of coho salmon (Farrell *et al.* 2001b). Specifically, a recovery box (Fraser box) was developed that included small flow-through channels in which captured coho were placed. Similar to the initial study, post-capture

coho were severely stressed and exhausted as revealed by comprehensive evaluation of plasma and muscle tissue. After placement in a recovery box for 1–2 h, coho showed significant metabolic recovery and improved swimming ability. Even more impressive was the revival of >90% of coho that appeared dead after capture. Post-capture delayed mortality was only 2.3%. As a result of these studies it was revealed that reducing handling time, careful fish handling and recovery in a recovery box significantly improve physiological status, swimming ability, and post-release survival. These research efforts led to the use of recovery boxes on most commercial vessels capturing non-target coho salmon. The specific mechanisms underlying this rapid recovery are still unclear, but seem to reflect increased rates of metabolite clearance and energy resynthesis (Milligan *et al.* 2000; Farrell *et al.* 2001b). In addition, it is not the stress or capture *per se* that caused the elevations in cortisol, but rather the post-stress inactivity (Milligan *et al.* 2000). Reduced bycatch mortality through physiological research has enabled more effective conservation of these sensitive fishes.

#### **Management issue: climate change**

The physiological response of Pacific salmon to environmental variability can affect stock productivity, survival and distribution. Ocean productivity, which is related to climate change, can affect salmon physiology. For example, low temperatures and decreased food availability or quality can impact the immune system and endocrine function of Pacific salmon (Larsen *et al.* 2001; Alcorn *et al.* 2003; Murray *et al.* 2003). Environmental conditions, such as sea surface temperatures, contribute significantly to the distribution and abundance of Pacific salmon (Finney *et al.* 2002). Modelling by Welch *et al.* (1998) suggests that global warming may severely restrict the ocean range of sockeye salmon. Field-derived thermal limits associated with sea surface temperature were used to estimate changes in seasonal distribution. Such changes would affect the viability of populations that utilize freshwater at the southern extent of their range and associated fisheries that depend on them. The authors speculate that the defined thermal limits observed are a consequence of attempts to maximize growth, or at least a response to conditions of negative growth. It is hypothesized that during times of low food availability, sockeye would move

to colder waters to reduce metabolic rate. To test this hypothesis and improve predictions of sockeye production and distribution, measurement of various physiological traits, such as growth and metabolic rate, along with location and environmental conditions, would be necessary. The potential implications of hypotheses proposed by Welch *et al.* (1998) illustrates the potential significance of climate change to Pacific salmon, particularly the reduction or loss of salmon stocks and species at the southern extent of their range.

Tolimieri and Levin (2004) evaluated correlations between Chinook salmon productivity and climate change. Results indicate that there is a likely effect of climate on Chinook salmon productivity. However, the response of different populations varied, suggesting that the unique life-history and physiological characteristics of each population may play a role in population-level response to climate change. Further, it is difficult to separate direct anthropogenic effects, such as dams, pollution, and habitat loss, with the effects of climate. Despite difficulties in identifying causal links between climate change and Chinook abundance, the potential effects of climate change suggests the need for precautionary management. Further evaluation of physiological and life-history traits of different Chinook salmon populations would improve the ability to resolve climate change effects and the relative influence of different overlapping anthropogenic influences. The level of anthropogenic contaminants in Chinook could resolve the relative influence of chemical pollution, evaluation of physiological condition of juveniles in freshwater could reveal the influence of habitat condition and dams, while measures of growth, condition and development in the ocean could improve understanding of ocean productivity and temperature effects.

### Conclusion

Because of the unique life-history traits of Pacific salmon and the complex physiological requirements to support these traits, the use of physiological information contributes significantly to effective management. Recent research continues to reveal the unique physiological capabilities of salmon and the role physiological measures can play in assisting the estimation of important management parameters (e.g. en route mortality, migration timing and distribution). Despite strong evidence

supporting the use of physiological information, the use of this information in efficiently and effectively assisting fisheries management is inconsistent and under-utilized.

A challenge of incorporating physiological information and monitoring in fisheries management relates to complexity of this fishery. A large part of the management challenge inherent in this fishery is the complexity of habitat, life-history traits and stock-specific physiological variability of Pacific salmon themselves. A further level of complexity is the multiple user groups, geographic regions and nations targeting fish from the same watersheds. The effective incorporation of physiological information in planning and monitoring could assist with management. However, the social complexities of the fishery may limit the ability of fisheries managers to focus on detailed biological information and effectively communicate management decisions based on such information to users and the public. Strategic use and effective integration of physiological information in key fisheries management measures, such as population size and en route mortality estimates, represent areas where physiological information could significantly improve Pacific salmon management.

### Case study – the grouper complex

#### Background on groupers

The grouper complex (subfamily Epinephelinae of the family Serranidae, including ~159 species in 15 genera) is an economically and ecologically important group of fishes that inhabit tropical marine environments (Heemstra and Randall 1993). These fish exhibit a diversity of life-history strategies and occupy a broad range of habitats. In general, they tend to be top predators (piscivores) on coral reef systems and exhibit slow growth, late reproduction, large sizes and long life spans (i.e. K strategists; Manooch 1987; Parrish 1987; Shapiro 1987). Groupers typically spawn in large predictable aggregations (Sadovy 1996; Domeier and Colin 1997), with some species changing sex during their lives (Policansky 1982).

Collectively, these life-history and behavioural characteristics make the grouper complex extremely vulnerable to exploitation from commercial, artisanal and recreational fisheries (Huntsman *et al.* 1999; Musick 1999; Dulvy *et al.* 2003). Indeed, many of the marine fish species currently on the

IUCN Red List are Epinephelinae and more recent assessments using the same criteria suggest that the majority of other Epinephelinae not previously listed are also threatened (Morris *et al.* 2000). As one specific example, the abundance of Nassau grouper (*Epinephelus striatus*, which are red listed by IUCN; Colin 1992) in the Caribbean has declined by as much as 80% since 1975 (Sala *et al.* 2001). A recent American Fisheries Society policy statement also summarized the imperiled status of those grouper species that occupy the waters of the south-eastern USA, the Caribbean and Mexico noting that conventional fisheries management strategies have been ineffective at protecting these fishes (Coleman *et al.* 2000).

### Physiology and management

#### Management issue: sex change, reproduction and exploitation

As the reproductive and life-history characteristics of these fish make them particularly vulnerable to exploitation, it is necessary to explore these issues in more depth. Many groupers belong to a group of marine fish that possess complex reproductive systems, including sex-change capabilities. Most groupers are protogynous hermaphrodites, first functioning reproductively as females and then later as males as they get larger. Sex change is essentially a physiological challenge, relying upon a number of physiological mechanisms believed to be mediated by social interactions (Devlin and Nagahama 2002). Perhaps the most important component of sex change is the endocrine system in which specific hormones act as messengers to stimulate physiological and anatomical changes (Bhandari *et al.* 2005), although the exact triggers are poorly understood (Nakamura *et al.* 1989).

Another important aspect of the grouper reproductive strategy is forming discrete spawning aggregations of many thousands of individuals (Smith 1972; Colin *et al.* 1987; Aguilar-Perera and Aguilar-Davila 1996). Groupers may migrate 100 km or more to reach spawning aggregations at distinct coastal sites (Bolden 2000). The exact cues used by groupers that lead fish to spawning aggregations and place them in a synchronous state of maturation are unknown. Most exploited populations, even those with low fishing effort, are female biased (Sadovy and Colin 1995), which likely influences mating behaviour. Because of the sequential her-

maphroditism, fishing actively selects for the larger, older and aggressive fish that are typically male (Coleman *et al.* 1996), thus exerting selection pressure on sexually mature females to become functional males.

Fishing spawning aggregations may alter a number of life-history characteristics by decreasing the size of the reproductive population, altering sex ratios and reducing recruitment, consequently lowering future productivity (Coleman *et al.* 2000). One of the biggest challenges in managing the grouper fishery 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. Also important are other basic life-history data including age and size at maturity and the sex-change schedule. In addition to the linkages between reproductive physiology and exploitation discussed above, the exploitation of mature adults can have other consequences. For example, new recruits often are unable to locate historical aggregations leading to the elimination of existing spawning units (Sadovy and Eklund 1999). At present, the physiological mechanisms associated with cues and direction finding ability are unknown. Information on how these animals choose and repeatedly locate spawning aggregations may provide conservation scientists with new tools or insight that could facilitate the restoration of previously decimated aggregations. Alterations in social habits and hierarchies could also be stressful, but at present that is only a hypothesis.

Without basic information on the 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. Physiological tools provide an opportunity to derive answers to these life-history-related questions that could greatly enhance management. Researchers developed a rapid and sensitive biochemical test for both sex and maturity of groupers based on the detection of a sex-specific blood protein (Heppel and Sullivan 1999). Working with gag grouper (*Mycteroperca microlepis*), Nassau grouper and red hind (*Epinephelus guttatus*), the authors used an enzyme-linked immunosorbent assay (ELISA) of the plasma protein vitellogenin

and developed an effective non-lethal test that could accurately determine sex and maturity. This advance enables fishers to collect and preserve small plasma samples on board from either fish that are going to be commercially harvested and eviscerated or released. Similarly, fish captured for research and monitoring can be enumerated and released without terminal sampling thus reducing unnecessary sampling mortality simply to determine sex and maturity. Simple knowledge of life-history characteristics such as sex ratio, maturity and sex-change schedules provided by this novel physiological approach has enabled managers to more effectively monitor and manage grouper populations. This approach is more risk averse than conventional management that relied on leaving large 'buffers' because of uncertainty in stock assessment estimates.

#### **Management issue: fisheries discards, physiological disturbances and mortality**

Another important issue associated with grouper exploitation is bycatch and discard mortality associated with these multispecies fisheries (Johnson *et al.* 1997). In commercial fisheries, some species are completely protected and must be discarded instead of harvested. In other commercial fisheries, regulations restrict harvest of certain size classes again necessitating release. Whichever the reason, it is clear that commercial fisheries do discard groupers but at present we know nothing about the consequences of discarding on individual physiology and survival, or population-level impacts. In recreational fisheries, groupers are also captured incidentally and intentionally and as such may be released either voluntarily or because of regulations. Although many fish are discarded, mortality rates of these released fish can be quite high. Physiological information has been used to understand why some species are more prone to angling-related mortality than others (Furimsky *et al.* 2003). In cases where stress is not lethal, sublethal physiological disturbances could also affect growth and reproduction (see review in Cooke *et al.* 2002; Cooke and Suski 2005). A recent report indicated that even very low levels of discard mortality (i.e. 1–5%) could have devastating effects on populations of long-lived species with low reproductive rates, such as groupers (see Schroeder and Love 2002). To date, there are surprisingly few studies that evaluate mortality or sublethal disturbances associated with either

commercial or recreational discard of groupers to determine the sustainability of these activities. Often, simple alterations in gear or fishing practices can dramatically influence the outcome of the capture and handling experience (Cooke and Suski 2005).

One challenge facing groupers that are discarded is that they are often captured at depth. When they are brought to the surface quickly, they experience rapid expansion of swim bladder gases leading to ruptured swim bladders, bloating, protrusion of internal organs and/or eyes and emboli (Burns and Restrepo 2002). Release mortality increases with depth of capture for groupers as they are physoclistous (Rogers *et al.* 1986). Some research has shown that several species of groupers (e.g. red grouper, *Epinephelus morio* and scamp, *Mycteroperca phenax*) can survive in some cases if they are rapidly returned to depth (Wilson and Burns 1996). Such information has been used to justify continued use of minimum size rules. Unfortunately, many fish experience severe bloating prior to release and become prey for seabirds and fish. Recent research has evaluated a shipboard venting technique for minimizing mortality in red grouper and gag. For both species, it appears that venting of swimbladder gasses prior to release can improve immediate survival of fish captured at depth (i.e. >21.3 m depth; Burns and Restrepo 2002). The same research team also did laboratory-based experiments using hyperbaric chambers to assess the mechanisms of mortality for only red grouper. Depths of swim bladder rupture in the hyperbaric chamber corresponded to depth of mortality observed in the field (Burns and Restrepo 2002). However, even fish that survive discard can experience a suite of effects. Earlier work by Di Marco and Marino (1999) revealed that capture of dusky grouper (*Epinephelus marginatus*) resulted in physiological disturbances in plasma biochemistry. Even fish that appeared healthy and were free of external lesions exhibited significant physiological disturbances post-angling. For groupers, stress from capture of fish in the wild is also highly relevant to attempts to collect broodstock for enhancement efforts (Di Marco *et al.* 1999). The long-term implications of capture-related stressors on fish growth, fitness or survival are unknown.

We contend that although very little is known about the consequences of capture and release on mortality or other sublethal effects, this is an area of research that would benefit immensely from greater inclusion of physiological information. Fisheries

managers require basic information on discard mortality and the factors associated with that mortality. Regulations can be altered or enacted if it is determined that certain gear or strategies have the potential to reduce stress and mortality. Information derived from integrated laboratory and field experiments have revealed depths at which fishing is not sustainable if fish are to be released (Burns and Restrepo 2002). Regulations that require venting could dramatically reduce mortality. Similarly, if it is determined that in some instances stress cannot be mitigated, then this may affect the choice of management strategies. Current efforts rely heavily on size regulations which may not be effective if small fish returned to the ocean die or have significant sublethal disturbances. Managers would also benefit from knowing the connection between the magnitude of physiological disturbance and effects on survival, fitness or growth.

#### **Management issue: stock assessment and understanding habitat–productivity–recruitment linkages**

At present, there are several examples of studies evaluating the environmental tolerances and physiological requirements of the early life stages of groupers in both natural and culture settings. These studies are relevant to understanding recruitment (e.g. identifying limitations) and also have relevance to understanding function of marine protected areas. Latitudinal shifts in spawning time may be related to water temperatures, consistent with a thermal preference (Colin 1992; Ellis *et al.* 1997b). Hatching rates and survival of larval grouper are typically optimal when fish experience minimum turbulence level for larval dispersions, high salinities, moderate light levels and stable temperatures (Ellis *et al.* 1997a,b) although different species do have different tolerances. Water temperature can markedly influence development rates and hence, dispersal potential, first feeding and survival in the field (Watanabe *et al.* 1995). Additional information on nutritional requirements, feeding and settlement/dispersal of early life stages would be informative (Grover *et al.* 1998; Colin *et al.* 1987). It is clear that high levels of density-independent mortality occur during the larval dispersal phase, largely because of variation in environmental conditions. Knowledge derived from laboratory-based aquaculture studies is helping to elucidate the specific environmental tolerances for wild popula-

tions of groupers and the effects on organismal physiology (Ellis *et al.* 1997a,b). Indeed, it is physiology that influences survival and growth of the early life stages and ultimately will play a major role in determining reproductive output and population characteristics.

Many of the issues associated with grouper habitat have some opportunity for integration of physiological information. For example, the South Atlantic Fisheries Management Council (SAFMC) developed a list of six generalized research needs relative to grouper habitat management (SAMFC 2006). We believe that all six research needs could benefit from the integration of physiology. For example, identification of environmental and habitat conditions that limit grouper production is important for management. As outlined above, fish ultimately affect the environmental relations of a fish and influence production. The SAFMC also identified the need to determine the relative effects of fishing, pollution and natural mortality on fishery population dynamics. At present, it appears that although physiological information could aid in understanding productivity and habitat relationships and steer management actions, it is rarely used for this purpose. Because stock assessment depends upon knowledge of life history, when data for a certain grouper species is unavailable, management agencies use data on other species with similar physiological traits and perceived tolerances. Thus additional information on environment, habitat and productivity relationships would benefit management and would require physiological data.

Current stock assessment techniques could also benefit from greater inclusion of physiological information. For example, information on reproductive biology would provide insight into the possible role of using stock assessment tools such as spawning potential ratio (SPR). Although currently used for groupers, this technique assumes equal numbers of eggs and zygotes which is likely not the case when males tend to be selectively harvested (Coleman *et al.* 1999, 2000). Until we know more about the reproductive biology of protogynous fish, this stock assessment tool is likely unreliable.

One of the most widely advocated management tools for grouper fisheries is the use of marine protected areas. However, we know little about exactly how they function (National Research Council (NRC) 2001). Marine protected areas

(MPAs) are the only strategy that effectively accounts for grouper longevity, slow growth, sequential hermaphroditic sex ratio, predictable spawning aggregations and extreme sensitivity to fishing (Coleman *et al.* 2000). However, long-distance movements can make reserve placement challenging. Efforts tend to focus on protecting spawning aggregation sites. The natural grouper mortality is low and it has been suggested that fishing mortality should be maintained at levels near natural mortality (Coleman *et al.* 2000). The challenge is in establishing a network of reserves that protects all life stages of these fish over large distances. This challenge can only be met if one understands the role of physiology in linking both organisms and populations to their environment. In the context of MPAs, physiology has the potential to influence population-level processes, especially those dealing with reproduction. Indeed, physiology will constrain the ability of target organisms to survive and reproduce in MPAs that do not include regions with appropriate environmental conditions.

When dealing with fisheries management issues, determinants of population size structure and growth must be considered. In the context of groupers, for example, somatic growth can be density dependent (Lorenzen and Enberg 2002), which has implications for the function of marine protected areas (Sánchez-Lizaso *et al.* 2000). Failure to understand links between environmental conditions, physiological characteristics, density dependence and growth would make it difficult to comprehend the complexities of MPA function and design. These ideas actually can be traced back to the early work of Beverton and Holt in the 1950s (See Guénette *et al.* 1998). This information on life history, physiology and density dependence is particularly useful for modelling simulations, which often occur early in the planning of MPAs (Gerber *et al.* 2003) or when assessing their function or interactions with fisheries (Holland 2002).

## Conclusion

A number of logical connections exist linking the physiology/life-history nexus and grouper conservation and management. We have noted several management issues and identified how physiology has improved management. For example, a number of tools have been developed to non-invasively assess sex and maturity. We also have a general understanding of sex change, and decompression

consequences for captured and discarded fish. However, relative to the challenges faced by these imperiled fish and the individuals and agencies that manage them, these are minor advances. We have identified a number of areas where physiology is not being used to its fullest potential and where there is greater opportunity for integration. The amount of physiological information known about most groupers is miniscule. We require better information on basic environmental relations and reproductive physiology for these fishes across all life stages.

If grouper managers fail to recognize the importance of life history and physiology, they will be more likely to fail in achieving their objectives because physiological processes associated with environmental conditions ultimately dictate the reproductive output and population dynamics in marine environments. Management actions such as implementation of MPAs must also include physiological considerations. For example, MPAs must be large enough to be resilient to catastrophic environmental changes or degradation that would constrain physiology and thus alter population dynamics. We, as well as the majority of managers who responded to our survey, contend that physiology could aid in the management of the grouper complex and should be used more often. We also want to acknowledge that there are examples of management issues that may not benefit from incorporation of physiology. For example, at present, there is excessive harvest capacity for groupers. Approaches that target direct effort reduction (e.g. permit reductions) will unlikely benefit from the inclusion of physiology.

## Case study – the tuna

### Background on tuna

Members of the family scombridae include highly migratory species with ranges that typically span from tropical to warmer temperate waters. Migration to higher latitudes and feeding forays into colder deep waters (Brill *et al.* 1999; Block *et al.* 2001; Gunn and Block 2001) are made possible by localized endothermy produced by high metabolic output, countercurrent heat exchangers and the axial position of aerobic muscles (Carey and Teal 1966, 1969). Temperatures can be elevated above ambient in several tissues, including the locomotor muscles, viscera and the brain and eyes. However,

the heart remains near ambient temperatures, thus limiting the amount of time tuna can spend in colder waters (Brill *et al.* 1999; Blank *et al.* 2002, 2004). Sizes within the scombridae range from an average of 0.5–1 m and 3–10 kg for the smaller species (Ramon and Bailey 1996; Doray *et al.* 2004) to the bluefin tuna (*Thunnus thynnus*) that can grow to more than 3 m and 600 kg over a 30-year lifespan (Magnuson *et al.* 1994).

Tuna are economically important species, supporting a commercial and sports fishing industry worth billions of dollars in the USA alone (National Marine Fisheries Service (NMFS) 2005). However, several species have been declining in numbers since the 1970s (Magnuson *et al.* 2001), and many unknowns remain about tuna life history and ecology. Recent physiological studies can be used to elucidate these aspects for tuna that inhabit spatially and geographically disparate waters. This information can help to improve the management of tuna populations by providing insight on the typical distributions and migration patterns of different tuna species (Sibert *et al.* 2003; Stokesbury *et al.* 2004), habitat use (Brill *et al.* 1999; Block *et al.* 2001; Gunn and Block 2001) and feeding efficiency and growth rates (Carey *et al.* 1984), among others.

## Physiology and management

### Management issue: overfishing, bycatch and post-release mortality

The fact that tuna generally are long lived and slow to mature (Baglin 1982; NMFS 2005) makes them more vulnerable to high levels of exploitation than fish with short lifespans. As well, tuna such as yellowfin (*Thunnus albacares*) can be more vulnerable to fishing gear during spawning events that do not follow a typical seasonal pattern, but rather occur during events of high food availability (Itano 2001). Currently, albacore (*Thunnus alalunga*), skipjack (*Katsuwonus pelamis*) and yellowfin stocks are generally considered 'fully exploited' while the northern and southern bluefin stocks are considered overexploited (Myers and Worm 2003). Based on the reviewed evidence, the probability of further stock decline for southern bluefin tuna is greater than in previous assessments (Commission for the Conservation of Southern Bluefin Tuna (CCSBT) 2004). Even so, catch assignments have not been reduced below 1999/2000 levels (International

Commission for the Conservation of Atlantic Tunas (ICCAT) 2004). One way that overexploitation of tuna stocks might be prevented and allowed to rebuild is to reduce the number of undersized/oversized tuna caught in fisheries. Currently over 210 species of sharks, skates, rays, teleosts, sea turtles, sea birds and marine mammals are listed as bycatch of the major tuna fisheries in the Atlantic Ocean and Mediterranean Sea (ICCAT 2004). Of these listed, 23 are species of tuna and bill fish. High numbers of tunas are released annually because of the federal imposition of quotas, minimum sizes and bag limits on offshore anglers (Skomal and Chase 2002). The NMFS implemented a number of time/area closures to reduce Atlantic tuna bycatch. A comprehensive analysis of the impact of these closures on tuna bycatch rates has not yet been performed.

A major problem concerning the live release of undersized and oversized tuna is how this should be performed to minimize stress. Currently, there is little information on the survival of tuna after capture and release. Although typically aerobic swimmers, tuna also possess large amounts of anaerobic white muscle that reach physiological limits during angling and subsequent air exposure. Few studies have been conducted to determine the physiological consequences of capture on post-release survivorship in tunas. For most fish species, high anaerobic activity because of angling causes homeostatic disruptions that can lead to behavioural changes and increase mortality (Brobbe *et al.* 1996; Nelson 1998; Millard *et al.* 2003; Cooke and Philipp 2004). Skomal and Chase (2002) found that angling stress in bluefin tunas also significantly increased plasma cortisol and lactate, and lowered blood pH while altering serum electrolytes. The degree of all the physiological changes was directly proportional to the length of the angling bout. Post-release recovery also consisted of limited vertical migration and lasted up to 2 h. The lone mortality reported out of the 135 fish caught was for the only fish not manually resuscitated prior to release. Unfortunately, it is unlikely that the results of this research will be incorporated into management because of enforcement limitations, such as trying to mandate short fight times that have been shown to minimize physiological disturbance in tunas (Skomal and Chase 2002). Nonetheless, agencies can use this information to educate the fishing public on ways to maximize post-release survivorship of tunas. A possible

integration of physiology information is the use of specialized archival tags to monitor key body parameters post-release. Domeier *et al.* (2003) accounted for a 26% mortality rate in released striped marlin (*Tetrapturus audax*) using archival tags. However, no physiological variables were measured so the causes of most of the mortalities were speculative.

#### **Management issue: population structure, assessment and conservation**

The ability to manage tuna populations to achieve optimum yield for fisheries has been severely affected by relevant social, economic and ecological factors. The latter has included debate over the classification of all tuna species as being 'highly migratory species.' While this status is warranted for northern and southern bluefin tuna that have large migrations between feeding and spawning areas, tagging studies have showed the scale of movements for many tropical tuna species to be quite limited (FAO 2003). Acoustic tracking and recent developments in archival tagging have provided new information on the horizontal and vertical distribution (as well as stock structure, movement and mixing) of bluefin tuna in the North Atlantic (Block *et al.* 2005). This information has shed light on the level of potential exchange between eastern and western stocks. Although this technology has yielded significant information on the physiological ecology of bluefin tuna (Block *et al.* 2001; Marcinek *et al.* 2001; Kitagawa *et al.* 2004; Block *et al.* 2005), it has only been deployed to a limited degree on other species of tuna (Block *et al.* 2003) such as bigeye (*Thunnus obesus*; Sibert *et al.* 2003; Kitagawa *et al.* 2004) and yellowfin (Block *et al.* 1997). Therefore, our focus will be on what is known about bluefin tuna populations and the importance of combining physiological and ecological information for their management and conservation.

Until recently, information on the location of bluefin spawning areas in the North Atlantic was incomplete, size at first maturity still is imprecise, and little is known about the frequency of spawning. Time/area closures are frequently discussed as an effective management technique. However, such approaches require knowledge that the tuna do not vary in their seasonal occupation of certain areas. Block *et al.* (2001) indicated annual migration routes and habitat use, including

breeding grounds, are necessary information for stock management plans (such as those used by CCSBT, FAO and ICCAT) that rely on low genetic mixing between tuna populations. Using electronic tags, they revealed that stock boundaries are regularly ignored by bluefin tuna. Recently, Block *et al.* (2005) further expanded on this population information, using depth and temperature data obtained from surgically implanted internal and external archival transmitters. They discovered the existence of two definitive North Atlantic bluefin tuna stocks with overlapping foraging ground, but discrete spawning areas primarily in the Gulf of Mexico and Mediterranean Sea. Because both populations are subject to fishing within their designated management units during the spawning season, Block *et al.* (2005) recommended protecting the populations using time-area closures to reduce direct and incidental catch. Further, they indicated the need for further spawning research and the need to determine the influence of physical and biological oceanographic conditions on bluefin movements.

Physiological information from electronic transmitters has been used to demonstrate the relationship of tunas to oceanographic conditions. Bluefin tuna are physiologically capable of dives to depths exceeding 1000 m and encounter temperatures from 3 °C while at their feeding grounds to 30 °C while spawning in Atlantic and Pacific oceans (Block *et al.* 2001; CCSBT 2005). Although they are able to enter these extreme habitats and maintain an internal temperature near 25–27 °C (Block *et al.* 2001), bluefin do show a preference for ambient temperatures ranging from 14 to 24 °C (Stokesbury *et al.* 2004). This preference is likely to help maintain optimal cardiac and muscle performance (Blank *et al.* 2004). Current stock assessment methods for Atlantic tunas generally do not incorporate this type of physiological information. However, this trend has been changing with the influx of new information concerning the complex interactions involved in tuna migration. This physiological information can be used to help quantify exchange rates between eastern and western Atlantic bluefin stocks. Used in combination with otolith biochemistry and genetics, managers will be able to better quantify common migration routes, timing and use of spawning areas, and validate the extent of stock mixing in the dynamic North Atlantic environment to improve management of remaining Atlantic bluefin.

## Conclusion

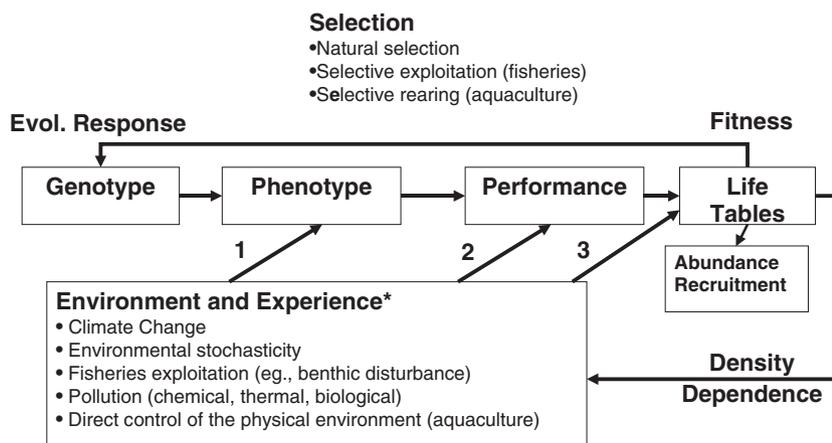
Current factors cited by people involved in tuna management and conservation that limits the application of physiological approaches are three-fold. They include the obvious difficulty in working with relatively rare and very large animals, the lack of adequate resources (time, money, and trained people) and results are incomplete as of yet and not viewed as being completely convincing by the international community. Further, it is difficult to directly integrate physiological information into stock assessment and management.

However, physiological studies can yield valuable information on tuna reproductive biology, feeding ecology, post-release recovery, sensory capabilities and thermal biology. In practice, the former variables may be used to develop hypotheses for assessment, plan fishing time-area closures, increase public awareness and promote conservation. Physiological information can provide a better understanding of preferred habitat of tuna and how changes in the ocean environment

might influence their distribution, thus providing useful insights for tuna fisheries management. The ability to repeatedly recapture individual tuna at fish aggregating devices (Doray *et al.* 2004) will provide opportunities for further exploring relationships between growth and relevant physiological variables.

## Integration and synthesis

We have explored the potential implications of the physiology/life-history nexus for fisheries management and conservation. Fig. 2 provides a summary of fisheries-relevant effects and management implications in the context of the physiology/life-history nexus. Our efforts focused on three case studies that spanned fish families with divergent habitats, life histories and management issues. In each of these case studies, we were able to identify a number of specific examples where information on the physiology of an animal provided a deeper understanding of their life-history responses and hence demography. As most of the fish we examined are



**Figure 2** The conservation and management of fisheries requires an understanding of the functions (boxes) and their influence on each other (arrows). Fisheries management is primarily concerned with population measures, such as abundance and recruitment. Traditionally, fisheries managers have relied on direct measurement or estimation of population measures. However, greater understanding of the effect of the environment on phenotype, performance and life tables improves the ability to predict and understand effects at the population level. Physiology is of primary importance in determining the response of individuals to the environment. The influence of the environment on phenotype, performance and life tables relevant to fisheries includes (1) changes in the environment can selectively disadvantage phenotypes – e.g. a climate regime shift may result in temperatures outside the optimal range of some individuals; (2) changes in the environment can decrease the performance of individuals – e.g. increased contaminant loads may impair osmoregulatory function and exercise capacity; air exposure of bycatch may cause stress and alter post-release survival; (3) changes in the environment can remove individuals, reducing abundance or recruitment – e.g. sedimentation may bury developing eggs; abrupt temperature changes may kill sensitive individuals at particular life stages. The figure was modified from Ricklefs and Wikelski (2002).

managed in terms of multistock or multispecies fisheries, stock assessment models depend heavily upon borrowing parameters from similar organisms. Often, these parameters have a physiological basis. In other cases, physiology provided more direct evidence of negative consequences associated with different activities (e.g. recreational catch-and-release fishing) and management decisions (e.g. assessing bycatch handling regulations). Collectively, these examples, albeit limited, highlighted the specific contribution of physiology to fisheries conservation and management. More importantly, we identified particular areas where there were opportunities for greater integration of physiology with applied fisheries science.

Several themes were evident throughout all of the examples presented. In particular, there was evidence that for many fish species there is significant information and research investigating either physiology or life history. However, there appears to be a lack of integration between this physiological information and life-history knowledge, and the application of physiology to the management of fish populations, communities and the ecosystems that support them. Research in freshwater aquaculture has improved our understanding of fish physiology and life history, although for marine fish, culture has been retarded by constraints in the understanding of the implications of life-history variation and physiology (Thorpe 1998). Typically fisheries management and conservation have focused on higher levels of organization (e.g. population) and specific life-history traits (e.g. growth and fecundity) with limited integration of physiological knowledge or relationships. The effectiveness of all of these disciplines would be improved by a better integration of all levels of organization, and acknowledgement of the role of physiology in influencing life history and behaviour. Research gathered within these disciplines should be more effectively presented to acknowledge their broader implications to the understanding of fish biology.

#### **Why have life history and physiology been poorly integrated in fisheries science?**

The paper by Ricklefs and Wikelski (2002) on the physiology life-history nexus has been widely cited during a short time period (61 times as of 19 February 2006 in Science Citation Index). From a taxonomic perspective, most of the studies that have

cited the paper were on birds ( $n = 26$ ), invertebrates ( $n = 9$ ), mammals ( $n = 7$ ), reptiles ( $n = 5$ ) and plants ( $n = 2$ ). There were numerous studies of a more general nature focused on theory that crossed taxa ( $n = 10$ ; Chown *et al.* 2004; Bonsall 2006). Interestingly, only one study of fish cited the Ricklefs and Wikelski paper [Grageda *et al.* 2005; the paper contrasted the life-history traits (e.g. fecundity, sex ratio, age at maturity and egg size) of two clonal strains of the mangrove killifish (*Rivulus marmoratus*) reared under common conditions]. Why do we see such few examples of this seemingly important nexus in the fisheries literature?

Although we did find some clear examples linking physiology with life history in fisheries science, the reality is that the majority of the literature on these topics is either decidedly focused on life history or physiology, rather than being integrative. There were even fewer examples of where knowledge of the life history and physiology was integrated to yield improvements to fisheries management and conservation. Why have these two topics been treated as independent for so long? Ricklefs and Wikelski (2002) suggest that previous thought about life-history traits has focused on the constrained evolutionary responses to the environment. They further suggest that differences in life history are driven by genetic differentiation, reflecting the optimization of phenotypes with respect to their environments, and that much less attention has been given to non-genetic responses to the environment. In the fisheries literature, there is perhaps better integration than in other fields, owing in part to the emphasis on production of fish using aquaculture. Aquaculture literature significantly improves our understanding of fish physiology, and in some instances, the relationship between physiology and life history. This information is not targeted to wild fisheries management or conservation. However, application of this knowledge can improve our ability to understand and manage wild fish. The literature evaluating the physiology and life history of exploited fish species is also abundant. However, the role of physiology in determining life history and broader population and ecosystem responses is only recently being considered important. Current efforts to assess the bioenergetic- (Beyers *et al.* 1999a,b) and organismal-level (Maltby 1999) responses to stress are particularly relevant for integrating information on physiology and life history.

In addition to the only recent recognition that life history and physiology are indeed linked, there are other factors that have retarded the ability of physiological information to improve fisheries management. One of the primary factors is the lack of interdisciplinary work among physiologists and fisheries ecologists/managers. At present, physiologists are viewed as laboratory dwellers, with little to offer fisheries management. We believe that this view is held by fisheries managers because of a lack of understanding of the paramount role that physiology has in survival and reproduction. Coincidentally, most work on physiology is conducted in academic settings and may therefore be viewed as having no practical fisheries management value. This is unfortunate as there is an increasing emphasis on field-based physiology, especially with fish models (Cooke *et al.* 2004; Costa and Sinervo 2004). Physiologists could also generate greater linkages to animal ecology and management by attempting to interpret their results in the context of whole organism physiology, even if the research was reductionist. Similarly, there is a need for more physiological research that addresses the link between individual physiological performance and population-level processes such as reproduction, competition and mortality. Ability to handle wild animals in laboratory settings has improved, but continues to limit research on some species. Coincident with all these issues are some fundamental institutional challenges such as a lack of funding for research that integrates physiology with life-history and fisheries management, as well as a lack of adequately trained staff. Only with more demonstrable and clear examples of specific management issues that have benefited from physiological research will these issues perhaps be resolved. It is our hope that this synthesis contributes to that outcome.

### Prospectus

The majority of the material cited in this synthesis is very recent, reflecting the current focus of research (we have not made a concerted effort to target only recent publications). Although the trends are promising, much more can be done to highlight the important links between physiology and life history. The first step may involve a fundamental shift in the education of scientists and managers. Although the recent primary literature is becoming richer with examples, most textbooks that serve as the basis for ecological teachings have yet to fully integrate

information on this topic (one clear exception is Spicer and Gaston 1999). The early work by Ricklefs (1973), more contemporary editions of that text (Ricklefs and Miller 1999), and texts by other authors, discuss interactions between behavioural ecology and physiology, or address other issues that integrate physiology and life history (e.g. allometry). However, there is no formal or clear acknowledgement of the direct links between physiology and life history, nor any applied connections. Even today, fish physiologists and life-history ecologists tend to work in isolation, publishing in different journals and attending different conferences, yet using the same model organisms. There is clearly a need for a more integrated biology with greater focus on physiological understanding. We anticipate much future work in this area as ecologists are identifying more fish species as appropriate models for testing life-history theory in the context of physiological constraints. Indeed, it has only been four years since the first paper explicitly identified the physiology/life-history nexus (Ricklefs and Wikelski 2002).

However, when one considers the integration of physiology and life history in the context of conservation and management, there are even fewer examples and less certainty. There are undoubtedly challenges ahead as researchers must convince managers, policy makers and even other scientists of the merits in incorporating knowledge of physiology into management actions and conservation strategies (Wikelski and Cooke 2006). This is true even though most of the existing decision support tools already rely on information on energetics and reproduction, immediately justifying this relationship. It will likely be some time before managers and conservationists are approaching physiologists looking for information to incorporate into policy (although there are some notable exceptions). However, there are many opportunities for physiologists to advocate the potential applicability of their data to basic ecological theory and applied management and conservation. We contend that there is a need to better link physiological characteristics with life history and other population-level parameters. Clear results from controlled experimentation (likely manipulations that would involve experimentally altering the physiology of fish) are needed to illustrate the direct connection between organism-level physiology and the population on a number of models to assist managers in understanding exactly how physiological information could

benefit their management and conservation activities. Although our efforts focused primarily on several groups of marine fishes, the integration of physiology and life history is equally applicable to other groups of fishes including those living in other aquatic systems.

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