

Physiology in the service of fisheries science: Why thinking mechanistically matters

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Abstract Behavioral responses of fishes to variability in environmental conditions and habitat quality are central to population-level demographic processes. Although field surveys can correlate abundance to habitat variables (physiochemical, biotic, and structural), they cannot provide mechanistic explanations. Moreover, field surveys are often stratified by time or geographic criteria relevant to humans, whereas fishes stratify by habitat variables relevant to them. If mechanisms underlying behavior are not explicitly understood, conclusions based on survey data can lead to biased inferences as to species-specific habitat requirements and preferences, as well as changes in

stock size occurring over time. Because physiology is the transfer function that links specific environmental conditions to behavior and fitness, we argue great gains can be made through the integration of physiology and fisheries science. These are complementary disciplines, albeit ones that generally function at very different temporal and spatial scales, as well as different levels of biological organization. We argue more specifically that integrating physiological approaches with behavioral studies and traditional fisheries survey data (where each approach develops hypotheses to be tested in the other) can mechanistically link processes from cells through populations to place fisheries management in an appropriate ecosystem context. We further contend that population- and species-specific mechanistic understanding of physiological abilities and tolerances can significantly help to: improve stock assessments, describe essential fish habitat, predict rates of post-release mortality, develop effective bycatch reduction strategies, and forecast the population effects of increases in global temperatures and ocean acidification.

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Introduction

Natural and anthropogenic changes to the structure and function of global ecosystems paint a future of

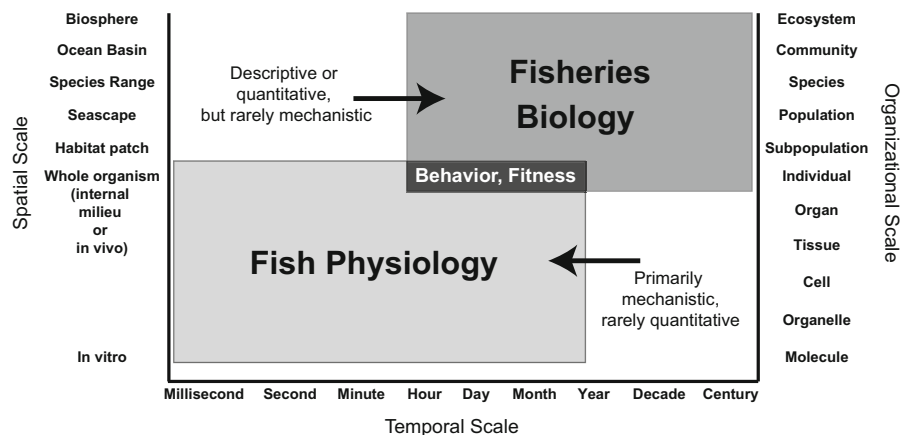
potentially unstable food security for humans (Rosegrant and Cline 2003). Global fisheries are simultaneously fishing down and farming up food webs to meet the ever-increasing demands for protein of a burgeoning world population (Pauly et al. 1998; Naylor et al. 2000; Jackson et al. 2001; Essington et al. 2006; Worm et al. 2009). Humans are thus demanding more productivity from aquatic habitats at a time when directional climate change and ocean acidification further threaten the health of aquatic ecosystems worldwide (Sumaila et al. 2011; Halpern et al. 2012). A sustainable future necessitates understanding the relationship of fisheries resources to environmental variation, including perturbations of anthropogenic origin.

In this synthesis, we therefore cover advances arising from a synergistic view of fish physiology and field fisheries ecology, first in the context of ecological sciences, and second, in the context of applied fisheries science. Fish physiology and fisheries science are complementary disciplines that function at different temporal and spatial scales, but are united at the study of individual behavior (Fig. 1). Fish physiologists typically investigate questions over temporal scales from milliseconds to seasons, and over spatial scales from the sub-micron to mesocosms, with a primary focus on cellular, organ, and organismal function. Such investigations typically try to identify cause and effect relationships, providing mechanistic insights at the level of the individual or below, but they may not scale to meaningful population and ecosystem contexts in isolation. By contrast, fisheries scientists (including ecologists and population biologists) typically investigate questions over temporal

scales of days to centuries; and over spatial scales from a habitat patch to ocean basins with a focus on populations, communities, and ecosystems. Fisheries science provides inferences that range from descriptive to highly quantitative, but that are rarely mechanistic in isolation (Smith 2002). We contend that synoptic understanding of the environment-organism-ecosystem interface will be greatly advanced through interdisciplinary collaborations between the mechanistically-driven physiological sciences, the pattern-oriented behavioral sciences, and the quantitatively-driven fisheries sciences.

The disciplines of physiology and ecology, whether through training, funding, or charge, differentially approach the fundamental versus applied science continuum. Physiologists have historically investigated questions that piqued their intellectual curiosity, often using a reductionist approach to minimize variation (Mangum and Hochachka 1998). Fishery biologists, in contrast, have traditionally conducted multivariable research more concerned with optimal or sustainable harvesting strategies (Ulltang 1998; Rothschild and Beamish 2009), or (more recently) with mitigating the profound effects that humans have on the living aquatic world (Halpern et al. 2008) and educating society about the need for resource conservation (e.g., Jacquet and Pauly 2007). It is long overdue for this dichotomy to be jettisoned because fertile interdisciplinary ground exists, especially when fisheries scientists consider directly the mechanistic basis underlying the hypotheses and field-observed patterns they are investigating, and when physiologists reach beyond reductionist approaches and univariate statistical analyses so that inferences can scale

Fig. 1 Complementary temporal, spatial, and organizational scales of fish physiology and fisheries biology. The intersection between these disciplines—the study of behavior and fitness (including growth, survival, and reproduction)—is fertile ground for collaboration



meaningfully to the population level. This incorporation, however, generally requires a detailed understanding of physiological principles that fisheries biologists—and of quantitative techniques and applied fisheries-relevant issues that fish physiologists—are generally ill-equipped to apply (by interest, training, and available resources) or many not fully appreciate. The direct interaction of the physiological and fisheries sciences, and collaboration with the ecosystem sciences, economics, and the social sciences, holds the potential to describe and forecast the effects of natural and anthropogenic changes on fisheries, and to address the societal concerns that operate at the scale of populations, communities, and ecosystems (Metcalf et al. 2012). Similar arguments are also being made for the integration of physiology, behavior, and ecology, especially as it relates to predicting the effects of anthropogenic activities (e.g., climate change, deforestation, pollution) on the world's ecosystems and preservation of critical ecosystem services (e.g., Chown and Gaston 2008; Denny and Helmuth 2009; Helmuth 2010; Sih et al. 2010).

In this synthesis, we briefly describe the potential for productive interdisciplinary collaboration between fish physiologists and fisheries scientists that will be necessary to place complex fisheries management issues in the appropriate organismal and ecosystem context. We also attempt to elucidate the mechanisms through which environmental variations are expressed in fish ecology and population dynamics via the inherent connections between individual physiology and behavior (Cooke et al. 2014). This synthesis is not intended to be comprehensively critical nor exhaustive. Rather, we seek to identify opportunities that can continue to bridge outstanding hurdles impeding interdisciplinary collaboration and focus those efforts, and we hope that practitioners of both physiology and fisheries science read this manuscript. This synthesis is structured to first investigate the need for understanding how fishes relate to their environment, then examine the relevant physiological frameworks that seek to explain how they do so. Following that, we provide an important section on potential discipline-specific biases and hurdles to collaboration before addressing several brief case studies of successful interdisciplinary research and presenting an appeal for integrative, iterative research uniting the two disciplines. Finally, although we note that fish physiology and the aquaculture field share a long history of

collaboration (e.g., Iwama et al. 1997), we focus this synthesis on the interactions between physiology and the field-based and quantitative ecological sciences.

The need for understanding how fishes relate to the environment

Defining how animals relate to their environment bears consequences for how the disciplines of physiology and ecology approach studying them, with clear implications for management and policy. Following the seminal work of Frederick Fry, fish physiologists have generally used an autecological approach to define how environmental resources and habitat affect an individual; whereas following the seminal work of G. Evelyn Hutchinson, fisheries ecologists and modelers generally follow a synecological focus on how interacting individuals and species affect the environment (Devictor et al. 2010). Fry (1947) elucidated the metabolic basis for behavior and activity in response to environmental conditions, defining the metabolic scope for activity (the difference between maximum and standard metabolic rates) as the net metabolic latitude an organism can apportion to growth, reproduction, and movement. This definition therefore allows the description of life history, ecology, and behavior in energetic terms. As we discuss extensively in a later section, the autecological perspective of Fry supports a comprehensive and utilitarian approach to ordering and measuring the effects of environmental variation on the functional capacities of organisms (Kerr and Werner 1980). In contrast, modern ecological approaches were shaped by Grinnell (1917), who formed the idea that a species' niche is the sum of habitat requirements and behaviors that allow it to persist and produce offspring. Elton (1927) approached the niche from a foraging perspective, positing that an animal's niche is its place in the environment in relation to its prey and its predators. Hutchinson (1957) moved the theoretical synthesis into multi-dimensional space and defined niche as the n -dimensional abstract hypervolume generated by assigning a metric to each environmental factor affecting the survival of an organism. The fundamental niche of a species is the region occupied by an organism in the absence of competitors (Hutchinson 1978), and the subset of the fundamental niche that an individual uses in the presence of its competitors is its realized niche.

We argue that both autecological (i.e., the study of an individual organism or particular species) and synecological (i.e., the study of whole plant or animal communities) approaches to describing habitat and environmental variation are important for effective fisheries management and governance, although both have large limitations. Spatial components that are central in two fundamental descriptors of habitat used in the study of biogeography (range) and U.S. fisheries management (Essential Fish Habitat, EFH) are unfortunately lacking in both approaches (but see Kearney and Porter 2009). The total geographic region inhabited by the sum of life stages of a species is its geographic range. In the USA, a subset of the geographic range with the appropriate habitat (waters and substrate) for positive fitness (breeding, feeding, and growth to maturation) for a given species is defined as the EFH and managed accordingly. Neither has a temporally- or ontogenetically-varying definition. As a result, fish of a given species are absent from their geographic range and EFH for much of the year, particularly fishes in mid-latitude temperate environments. One might hope to improve upon the geographic range or EFH designations of habitat with autecological or synecological modifications, but both Fry's focus on fish energetics and Hutchinsonian niche level definitions lack spatial and temporal bounds. The fundamental niche is a varying subset of the EFH, and the realized niche is a varying subset of the former; but in practice both change over ontogeny and in space and time. We argue, as have others (e.g., Kearney 2006), that mechanistic understanding of niches is required to predict distribution, but niche-based descriptors of fish-habitat are presently difficult to incorporate into spatial fisheries management. Despite their limitations, Fry's autecological and Hutchinson's synecological perspectives have collectively led their disciples to investigate different scales of biological organization along the organism-environment interface; their potential congruence invites synthesis (Kerr and Werner 1980). Hutchinson's synecological perspective provides an appropriate context for embedding Fry's concepts within a niche structure, defining the Fry-Hutchinson niche as the hypervolume defined in units of an organism's scope for activity, both in the absence or presence of other species (Kerr and Werner 1980).

Modern quantitative approaches, including the Metabolic Theory of Ecology (MTE), Dynamic

Energy Budget (DEB), and Species Distribution Models (SDM), may elegantly bridge the divide between autecology and synecology by providing both mechanistic and quantitative explanations of the organism-environment interaction, but their complexity can serve as an obstacle to adoption by both fish physiologists and fisheries scientists. West et al. (1997) noted that metabolic rate is limited by the transport of materials through an organism's fractal, branching circulatory system. The theory posits that metabolism is the fundamental biological rate shared by all organisms, and thus governs most of the observed patterns in ecology. MTE is thus a unifying theory driving pattern and process in biology, from cells through all the levels of the biosphere (Brown et al. 2004), synthesizing top-down, ecosystem-level, and bottom-up organismal-level approaches (Schramski et al. 2015). Similar scaling is possible using the DEB theory for metabolic organization developed by Kooijman (2001). This mechanistic model attempts to explain biological dynamics from cells to populations across a wide range of organismal biodiversity via a mass balance energy approach of individuals (Nisbet et al. 2012; Kooijman 2001; Martin et al. 2012). The DEB model has several advantages including: relying on simple physiological principles common to all species, a limited number of parameters that integrate genetic and environmental effects on the animal, and a structure that allows for the integration of different time scales (including ontogeny and evolutionary time) (Alunno-Bruscia et al. 2009; Martin et al. 2012). A problem in its application, however, is that many of the underlying processes are intimately interlinked, complicating the study of individual processes or their contributions (Kooijman 2010). Recent DEB extensions link to bioenergetics (Nisbet et al. 2012) and individual based models (IBM; Martin et al. 2012). Finally, SDMs use spatial ecological data to predict species range and habitat suitability, and can be parameterized with physiological data to offer a mechanistic view of the fundamental niche that can be mapped in a landscape context for robust mechanistic insights (Kearney and Porter 2009). Collectively, DEB, MTE, and SDM models show potential for interdisciplinary collaborations between fish physiologists and fisheries scientists, though notable challenges exist in obtaining the requisite data to parameterize them (Sousa et al. 2010). Improved mechanistic understanding of the fish-environment

interface and how it changes in space and time is needed for these quantitative approaches to render realistic and meaningful outputs that can be comprehended by stakeholders and applied by resource managers. We will focus on the Fry (1947) paradigm in this synthesis, as we believe that it is the most conceptually approachable and practically applicable conceptual framework to unite physiologists and fisheries scientists at this time.

Linking environmental conditions to behavior and fitness for improved mechanistic understanding

Physiology provides a “fish-eye” view of the environment and the tradeoffs faced by individuals as they make decisions with fitness consequences, because physiological abilities and tolerances are the transfer functions that directly link organisms (and eventually populations) to their environment (Fry 1971; Weissburg and Browman 2005; Jusup et al. 2011). In the following sections we examine how environmental variables are detected by fishes, how they scale to behavior and fitness, and how physiologists must overcome discipline-specific hurdles to disentangle the fish-environment interface.

Physiological processes reflect an organism’s internal ecology; an interacting milieu of cells, tissues, and organ systems, each with their own defined roles that act within a broader ecosystem—the individual—that can scale to populations and ecosystems through effects on individual fitness (Weissburg and Browman 2005). Disruptions to this balance lead to departures from homeostasis, inhibiting fitness by affecting survivorship, growth, or reproduction. Fishes respond to such deviations via complexly interacting biochemical, neurological, endocrine, and behavioral feedback mechanisms (Ricklefs and Wikelski 2002). Fishes sample their immediate environment with a sophisticated suite of sensory receptors tuned to solutes, gasses, temperature, bulk flow, electrical, and magnetic fields, as well as light, acoustic vibrations, and textures (e.g., Kapoor and Hara 2001; Sloman et al. 2006; Hara and Zielinski 2007). Selective pressures operate strongly upon the functional characteristics and distributions of these receptors according to species-specific life histories and tasks (e.g., Ladich et al. 2006; Horodysky et al. 2010, 2014; Kaijura et al.

2010; Kalinoski et al. 2014). Biotic and abiotic environmental stimuli are measured by these sensors and are transformed into behavior (Weissburg and Browman 2005). The interplay between the sensory, neural, and motor systems renders environmental conditions actionable at the organismal level. The behavioral acts of an individual in response to its need to maintain internal homeostasis and experience positive fitness, when iterated over a multitude of similarly acting animals, effectively translate into ecological processes (Fig. 2). Sensory physiology thus provides a second mechanistic link between environmental variation and ecological patterns (Spicer and Gaston 1999; Seebacher and Franklin 2012; Healy et al. 2013). It is often assumed (but not always correctly) that, while measuring and interacting with the surrounding environment, individuals behave and select habitats in ways that maximize their fitness in the manner in which natural selection iteratively operated on their ancestors. In modern times, natural and anthropogenic habitat change and fishing pressures exert additional selection pressures that may amplify, cancel, or override natural ones (Edeline et al. 2007).

Ultimately, the habitat selected by a fish both determines, and is determined by, its triptych physiology-biochemistry-morphology matrix (Claireaux and Lefrancoise 2007) that defines the form-function-environment interdependence. This occurs because individual and adaptive responses to environmental variation are limited by physical, physiological, and phylogenetic mechanisms (Fry 1947; Ricklefs and Wikelski 2002). Many physiological and ecological components of fitness express across a fish’s life history through the processes of survival, growth, maturation, and reproduction, affecting both stock reproductive potential (adults) and recruitment (larvae and juveniles) processes (Trippel 1999; Carlson and Seamons 2008). Similarly, there are many fitness tradeoffs over the course of a lifetime as fish balance: foraging versus predation risks, energy gain versus expenditure, the implications of early versus delayed maturation at small versus large body sizes, emigration versus tolerance of gradients of suboptimal environmental variables, and so on (Mangel and Stamps 2001). In cichlids, pupfishes, salmonids, sticklebacks, and sunfishes, there may exist multiple intraspecific resource polymorphisms and varying behavioral and life history strategies that reduce competition via resource partitioning, sexual selection, and/or

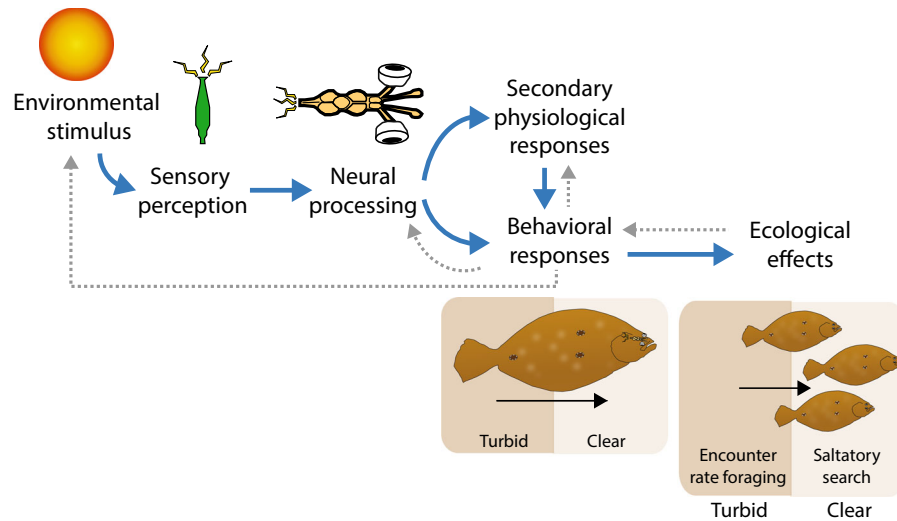


Fig. 2 The behaviors of an individual in response to its physiology, when iterated over many individuals, become the ecologies of populations (Weissburg and Browman 2005). Physiology provides the mechanistic link between environmental change and ecological patterns (blue arrows), subject to feedback modulation (grey dashed arrows) (Scott and Sloman 2004; Seebacher and Franklin 2012). In this hypothetical example, abiotic environmental stimuli (photons of light) are received by photoreceptor cells of an individual flatfish; information is passed through and processed by the neural system, resulting in an individual's behavioral response to seek brighter conditions. The movements of multiple light-limited

individuals from turbid to clear water enables a population-level shift from energetically-costly encounter-rate feeding to more energetically-favorable visual ambush foraging (i.e., population-level and ecosystem-level effects; Utne-Palm 2002; Mazur and Beauchamp 2003). Several studies of different flatfishes show increased up-estuary movements and activity in the shallows on (clearer) flooding tides, and down-estuary movements to deeper waters during (more turbid) ebbing tides associated with the balance between foraging and predation risk (Wirjoatmodo and Pitcher 1984; Gibson 2003; Capossela et al. 2013; Furey et al. 2013)

improved reproductive access (Gumm 2012; Skulason and Smith 1995). There are thus strong links and numerous feedback mechanisms (from the molecular to ecosystem level) between individual physiology, fitness, and life histories of fishes (i.e., the “physiology/life history nexus”; Ricklefs and Wikelski 2002) that can be used to optimize fisheries management initiatives if placed in the appropriate mechanistic context (Young et al. 2006).

Physiological classification of the environment

In his classic monograph, Fry (1947) investigated environmental conditions directly affecting the metabolism of organisms, defining a set of functional linkages. Based on their potential effects on an individual's metabolic scope, Fry's paradigm classified environmental factors into five categories: (1) controlling, (2) limiting, (3) masking, (4) lethal, and (5) directive. Metabolic scope is thus reflective of an individual's scope for fitness (i.e., growth and

reproduction), within which all metabolic requirements must be met (Fig. 3a, b). Controlling factors (e.g., temperature) govern biochemical reactions and set standard and active metabolic rates. Limiting factors (e.g., oxygen, pH) interfere with the ability of the cardio-respiratory system to deliver oxygen and metabolic substrates to the tissues, reducing active metabolic rate, and constraining metabolic scope until (at the extreme) they exceed physiological tolerances and become lethal. Masking factors (e.g., salinity) raise the metabolic costs of maintaining homeostasis. Lethal factors (e.g., pollutants, disease) proscribe metabolism and result in organismal death. Finally, directive factors (e.g., light levels) shepherd animals toward habitats that better match either sensory abilities or physiological requirements. Controlling and limiting factors can also be directive; the latter allowing fishes to exert some degree of behavioral control over the effects of environmental conditions.

Heuristic extensions of Fry's paradigm by Neill et al. (1994) and Miller (1997) have conceptualized

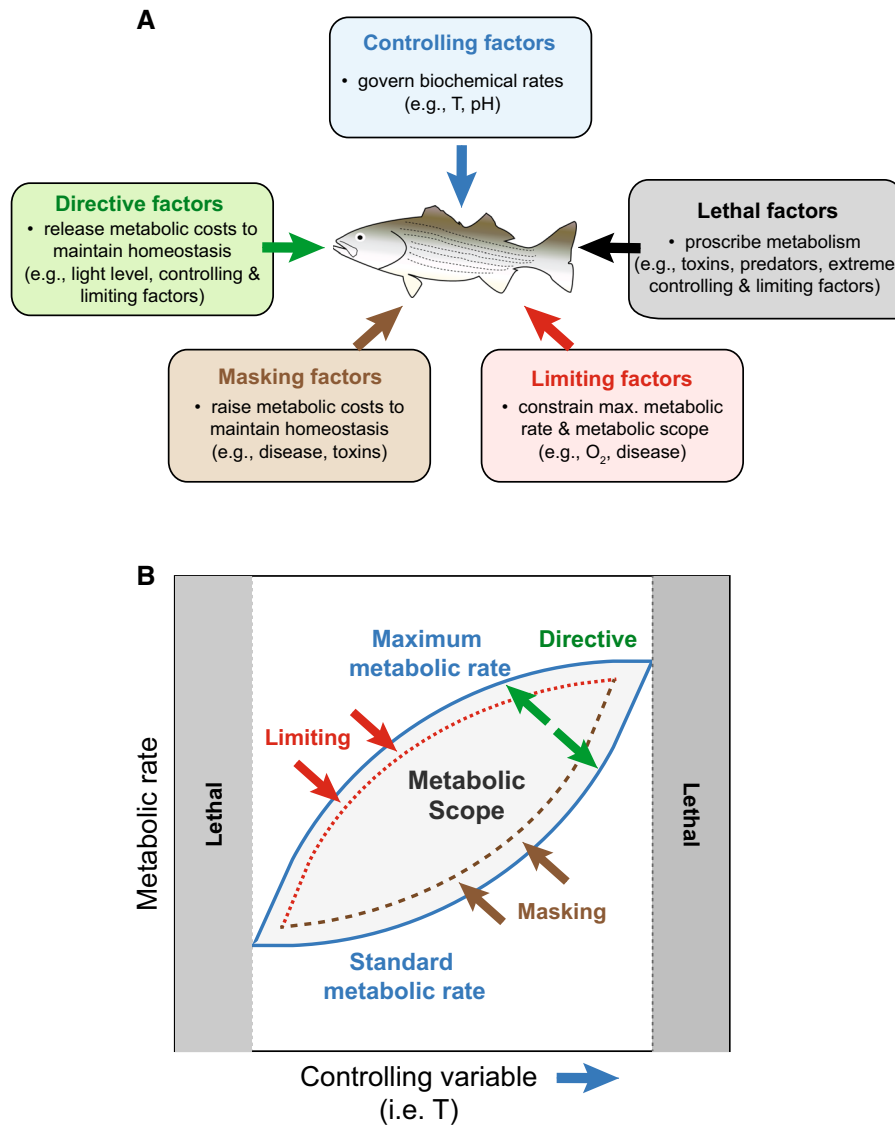


Fig. 3 **a** Physiological classification of environmental variables according to Fry (1947), including controlling (blue), lethal (black), limiting (red), masking (brown), and directive (green) factors. **b** The prospective effects of a controlling variable (in this instance temperature, T) on individual's

standard (lower blue line) and maximum metabolic rates (upper blue line) and metabolic scope (range between standard and maximum active metabolic rate, shaded grey oval) (adapted from Fry 1947; Neill et al. 1994)

the effects of environmental factors on levels of organization beyond individuals to populations. Their collective synthesis represents generalized relationships with varied levels of empirical support, many interesting exceptions, and tremendous complexity. Energetic consequences of environmental conditions iterate over individuals (subject to feedback modulation) to contribute to population demographic processes such as growth and reproduction (e.g.,

fecundity, egg size and quality), and ecosystem characteristics such as species diversity.

To understand physiological abilities and tolerances is thus to gain insight into the mechanisms underlying individual behavior and the resilience of life history strategies to both anthropogenic and natural environmental changes over time and space, particularly if paired with other disciplines such as hydrography, behavior, evolution, and genetics. It is therefore

tempting to directly scale individual physiology to population or ecosystem processes. However, scaling of the relationships between environmental conditions, individual physiology, and population effects is often complex; linkages are not simply additive as biotic and abiotic factors and feedbacks affect individual, population-level, and landscape-scale responses to environmental variation (Miller 1997; Metcalfe et al. 2012). In other words, a population response is not merely the sum of individual responses due to feedback mechanisms operating between individuals (consider, for example, the Allee effect and other frequency- and density-dependent processes), and among populations and the environment (Miller 1997). The focus of Fry's paradigm on energy flow across all levels of organization, as modulated by environmental conditions, renders it an exciting template for the interdisciplinary integration of fish physiology and fisheries science (Neill et al. 1994; Claireaux and Lefrancoise 2007), particularly if packaged in a Hutchinsonian ecosystem context, thus providing a means by which physiology can help generate management and policy-relevant knowledge (Cooke and O'Connor 2010).

Overcoming interdisciplinary hurdles: bias-avoidance caveats for physiologists and fisheries scientists

Fishes are exposed to multidimensional environmental conditions that simultaneously vary and interact. This complexity is difficult to replicate adequately in the laboratory, to control in the field, or even to model with a computer absent mechanistic a priori knowledge (Claireaux and Lefrancoise 2007). Yet, the behaviors and interactions of an organism within its selected habitat can have profound consequences for its physiology, life history, fitness, and population demographics, as well as ecological interactions (Huey 1991). There is, however, a difference between tolerating environmental conditions and selecting ones that provide a fitness benefit. The term "tolerance" can be used to describe the distributional extremes of physicochemical variables that can be endured by a species without lethal outcomes (Jobling 1981). Fry's (1947) controlling, limiting, masking, and directive factors can be tolerated by a species except at their extremes, as can some lethal factors in brief infrequent exposures.

Several other terms are used (and sometimes abused) by physiologists and fisheries scientists to describe how fishes relate to environments, ecosystems, and habitats. In order to ascribe the phrase "habitat use" to the behavior of a fish, the physicochemical and biotic properties of the water column specifically used over time must be known. In the literature, environmental or habitat preferences are too frequently a case of environmental or habitat experience; the latter being a measured variable that is a consequence of the habitat selected without being a mechanistic driver of behavior. Under this scenario, what appears to be habitat preference may simply just be habitat use, ignorant of alternative habitat configurations in the environment. Habitat selection is the proportional use of a given habitat relative to its availability, and offers improved ecological insights relative to habitat use. This measure has been assumed as an indicator of positive fitness consequence, but is only a derivative proxy of habitat preference that lacks an explicitly defined mechanism. A habitat requirement is a characteristic of a habitat that the animal needs to experience positive fitness, and may be defined by an organism's physiology, life history, or behavior. To ascribe the term "habitat preference" to a range of a given physicochemical variable selected by a fish, we must know: (1) that the fish is making a decision on the basis of that factor and not another unrelated or covarying parameter(s); and (2) that it selects the specific magnitude of that variable among other available values. A preferred temperature, for example, is the temperature to which individuals of a species given free choice would characteristically gravitate over time regardless of their acclimation histories, presumably because this temperature maximizes metabolic scope (Fry 1947; Beitinger and Fitzpatrick 1979; Jobling 1981; Ohlberger et al. 2008). Predator-prey interactions also play an important role in determining how fishes relate to habitat, with each of these actors balancing individual physiology (i.e., homeostasis, stress, sensory ecophysiology, energetics) and behavioral ecology (i.e., predator avoidance, optimal foraging) in the predator-prey arena in the interest of fitness (Hugie and Dill 1994; Ahrens et al. 2012).

There are, however, two additional important caveats to the overall view of habitat selection: (1) fishes only have knowledge of their immediate environment; and (2) fishes can only truly prefer an

environmental variable they can sense and where there is a linear (or at least a direct and stationary over time) relationship between receptor and/or afferent nerve activity and the physical variable. For example, species-specific depth “preferences” are frequently a concern in population assessments of large pelagic fishes (e.g., Block et al. 2001; Evans et al. 2008; Ward and Myers 2005). But we contend, as have others (Bernal et al. 2009), that the concept is mechanistically nonsensical. Although hydrostatic pressure receptors (which theoretically could provide fishes with a sense of depth) have been demonstrated in an elasmobranch (Fraser et al. 2008), the receptors display response characteristics that are neither linear, nor direct, nor stationary over time, indicating that they would be incapable of providing an absolute sense of depth (although they could sense acute changes in hydrostatic pressure). Many fishes, however, express their life histories at a “depth range,” which is likely a mechanistic interaction between light, temperature, and oxygen conditions and prey or predator dynamics at the covariate variable depth. Similarly, while the masking factor salinity has been traditionally heralded as a determinant of faunal distributions in coastal waters (Bulger et al. 1993), it covaries with a number of controlling, limiting, masking, and directive physicochemical variables in estuaries. Untangling a mechanistic response to the salinity from its covariates requires a reductionist laboratory approach using physiological research procedures (e.g., Nearing et al. 2002; Loretz 2008). Similarly, predator and prey abundances are often correlated, but if one cannot be detected by the other under the environmental conditions at the time, they are as meaningless to the acting organism as unknown and undetected habitats. We often lack rigorous understanding of which (and when) environmental and biological parameters are true signals that affect fitness, performance, and survival, and which (and when) they are noise (Helmuth 2009).

Collectively, because fish physiologists and fisheries scientists work at different scales of organization (e.g., Fig. 1), the questions of interest, appropriate sampling strategies, and motivations to elucidate the relationships of fishes to environmental conditions are different and subject to different levels of bias. Attempts to understand fish ecology and habitat requirements are often derived using correlations between physicochemical measurements and catch

rates from field surveys using stratified random sampling designs (e.g., Braaten and Guy 1999; Kupschus and Tremain 2001). Biases may result, however, from the substantial differences between the stratification strategies used by fishes and the researchers studying them (Fig. 4). For example, for reasons of simplicity or due to logistical, economic, or political constraints, scientists studying fishes stratify their sampling by spatiotemporal relevance to humans, but not fish. Such human-centric stratifying variables include geography, depth, and time.

By contrast, organisms can only experience their immediate microhabitat (Helmuth 2009), thus fishes stratify themselves by the physicochemical variables they can detect in their immediate surroundings given their sensory mechanisms. We argue that these are largely limited to: (1) temperature, (2) oxygen, (3) salinity, (4) light and day length, (5) substrate (bottom type, vegetation, places of refuge, etc.), and (6) effective prey abundance. The last of these is a function of the number of prey and their availability to the predator. Prey availability is a reflection of the match/mismatch of the fishes’ sensory abilities and the visual, olfactory, and auditory environments. An important consideration is that many environmental factors, including turbidity, anthropogenic chemicals, noise, and light pollutants, can affect prey availability by attenuating detection range by reducing the signal:noise ratio (i.e., sensory pollution) (Scott and Sloman 2004; Slabbekoorn et al. 2010). Correlations or multivariate associations of field-measured physicochemical variables to fish abundance and behavior can thus be fraught with bias. Nearly any biological pattern will correlate with a number of biotic and abiotic patterns (Seebacher and Franklin 2012); whether the relationship between catch and a given variable is mechanistically causal, covariate, or occurs by chance is another question. For that reason, simple niche-level environmental parameters experienced by an organism may not correlate well with the habitat-level proxies (or their covariates) measured by humans and used in correlations (Helmuth 2009), requiring further mechanistic investigation beyond the simple correlation.

While environmental factors shape the distributions of fishes at multiple spatial scales (Furey et al. 2013), stratifying fisheries surveys by a given day’s oxygen or temperature distribution in the waters to be sampled is a nontrivial and potentially nonsensical task (consider

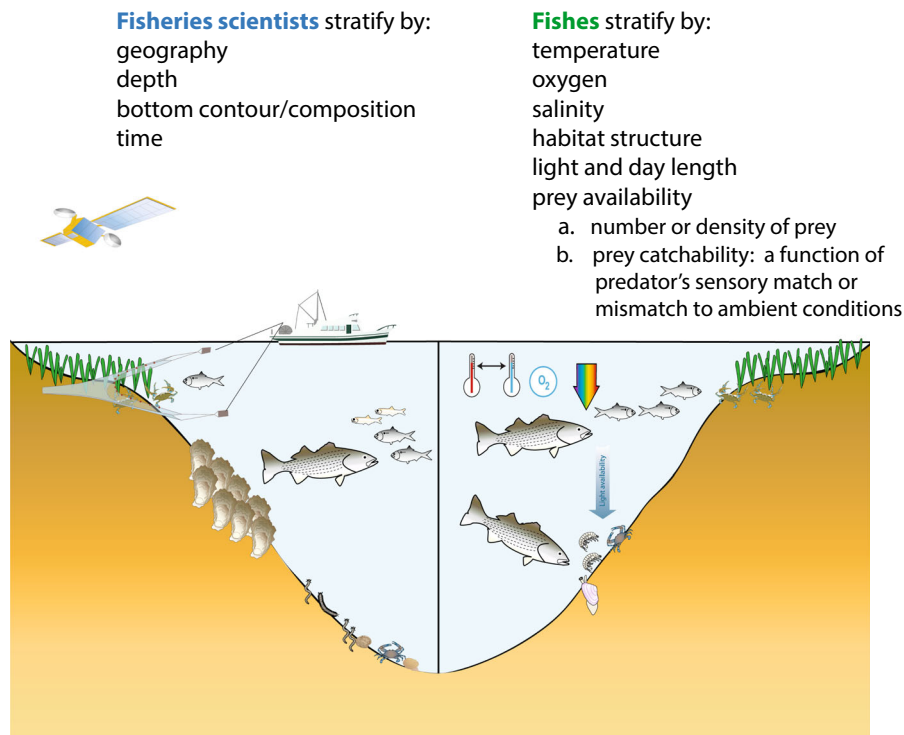


Fig. 4 Different stratification strategies used by fishes and fisheries scientists. Fisheries scientists frequently stratify their sampling by spatiotemporal criteria (e.g., geography, depth, bottom contour or composition, and time) that are relevant to humans for practical and management purposes. By contrast, fishes stratify by variables they can detect, including

physiochemical properties (temperature, oxygen, salinity, light level, day length), habitat conditions (substrate bottom type, vegetation, refugia, etc.), and effective prey abundance. The former is a reflection of the match/mismatch of the fishes' sensory abilities and the visual, olfactory, and auditory environments

the effects of wind and tides). This fundamental disconnect between how fisheries survey schemes are often organized (e.g., random stratified design by geographic area and date) and what actually organizes the distribution of fishes can lead to fatal flaws in inference, to the detriment of population and ecosystem management. Specifically, failure to consider explicitly or to measure the actual mechanisms driving fish behavior can lead to dangerous tautologies. As discussed by Brill (1994) and Brill and Lutcavage (2001) for tuna fisheries, this is especially true when catch/abundance proxies are used to determine the effects of environmental conditions on catch or abundance. While it is tempting to infer that a species “prefers” a given physicochemical condition under which catches were high, the inference is circular reasoning at best, and may be fundamentally flawed if the fishes have aggregated (or were more susceptible to capture) for reasons other than the measured variable of interest that happened to correlate to high

catch (Lynch et al. 2012). Demonstrating environmental preference is thus difficult to accomplish with a survey alone. For example, light levels affect foraging, schooling, and ontogenetically-specific gear escape-ment of walleye pollock (*Theragra chalcogramma*) from trawl gear (Kotwicki et al. 2009). Failure to consider the mechanistic effects of light on behavior in this case would result in undocumented changes in catchability and gear efficiency, decoupling the proportionality of catch and abundance. A logical interaction between physiologists and fisheries scientists is thus the study of habitat-mediated gear bias, potentially using telemetry, as the manner in which fishes react to gear depends on their physiology, the environmental conditions, the structure of the environment, and manner in which the gear is fished.

Telemetric and biologging technologies (herein called electronic tags) have revolutionized scientific understanding of the movements and habitat use of fishes in a manner very complementary to field

surveys (Rutz and Hays 2009; Cooke et al. 2012a; Metcalfe et al. 2012; Crossin et al. 2014). Electronic tagging offers the capability of recording an animal's behavior while simultaneously recording certain physicochemical properties to which the tag (and thus, the fish) is exposed (Metcalfe et al. 2012). Physiology can determine potential effects of tagging techniques on animal stress and behavior (Bridger and Booth 2003), and tags can provide critical habitat use data from the perspective of a fish in ways no other technology can (Hussey et al. 2015). Moreover, when electronic tagging and remote sensing of environmental variables are combined with physiological insights from laboratory experiments, the observed behaviors can be mechanistically explained, supporting reasonable extrapolations regarding behaviors in other environments or areas. Powerful examples of this union include the explanation of the vertical movement patterns of tunas and other pelagic fishes via the effects of temperature on cardiovascular performance (Brill et al. 1999; Galli et al. 2009), the expansion of vertical habitat enabled by the visual thermophysiology of swordfish (Brill et al. 2005), and the effects of varied physiological stressors on migratory behavior in salmon (Hinch et al. 2009). However, it is difficult to ascribe “preferences” solely on the basis of electronic tagging because tag sensors only measure the physicochemical properties immediately surrounding the fish. While the habitat characteristics used by the fish are thus known, it remains unclear from what available options the fish may have selected. However, the term “preference” can be ascribed to the conditions selected by animals when tags are paired with other field measurement technologies that simultaneously describe the available water column properties from which the tracked fish may have chosen (Cayré and Marsac 1993; Josse et al. 1998; Brill et al. 1999). Thus physiology can complement biologging technology by providing context regarding a fish's actual area of inference—the spatiotemporal area from which it makes its habitat choice.

Laboratory studies of individuals can provide a rigorous though reductionist mechanistic understanding of how individual variables drive fish physiology and behavior, identifying organismal niche spaces with regard to environmental variables, but run the risk of limited real-world applicability. As physiologists generally investigate individuals and/or their

parts, organisms must be collected and data analyzed in a manner that is representative of the population of interest, especially if inference is to be extended beyond the exact subjects being studied. Sample organisms must be randomly selected from relevant populations of interest that are explicitly defined, with care taken to represent any variation in ontogeny, sex, or location relevant to the question. For example, cod physiology is profoundly affected by temperature, but different populations of cod respond very differently to thermal gradients and express different life history characteristics (Colosimo et al. 2003; Pörtner et al. 2001; Metcalfe et al. 2012). The selection of the appropriate cod depends on the nature and scale of the very question itself—not just any cod will do. Further, as physiologists often take repeated measurements on each subject, the within-individual variability inherent in this approach must be modeled to avoid issues of pseudoreplication and inflated errors in any hypothesis tests (Hurlbert 1984; Rosenberger and Chapman 2000; Horodysky et al. 2011). In comparative studies, great care must be taken to ensure methodological consistency of variables known to affect rates (i.e., temperature, oxygen), particularly when acclimating animals or comparing fishes with different physicochemical histories and niches.

Wild-caught individuals used for physiological experiments must also not be held in captivity for too long lest they no longer represent ‘wild’ fish, and researchers in all fields should diligently ensure the ethical treatment of subjects at all experimental stages (collection, husbandry, experiments, euthanasia), reducing stressors that may render the subject unusable or mask the physiological technique or behavioral assay employed. For example, the composition of the diet fed to fishes in captivity can significantly affect respiratory and cardiovascular physiology (McKenzie 2001). While the need for fish to exhibit “wild” characteristics may vary depending on the question in physiology, it is often of paramount importance in ecology. The needs of ecologists to understand the limitations of a wild fish can thus be undercut by physiologists' reductionist demands for acclimation to reduce variability in physiological response. Laboratory experiments can produce unambiguous (but reductionist) inferences via single or dual-variable assays, but with potentially limited applicability to real world problems of multidimensional simultaneously interacting variables. Via collaboration, both

goals can be met—physiologists can explicitly describe the trade-offs made by ecologists in selecting and acclimating animals to reduce variability outside of the primary research question, while ecologists can assist physiologists to maximize a study's frame of inference and enhance real-world applicability of laboratory experiments. When appropriately applied, and especially when paired with behavior, electronic tagging, and/or field measurement, physiological tools can both identify specific mechanistic drivers of behavior [e.g. homeothermy in salmon sharks, Goldman et al. (2004); migratory behaviors in salmon, Cooke et al. 2008)] as well as eliminate other explanations that, while correlative, are not causative.

Case studies of physiology in the service of fisheries science

In addition to the complex of form-function-environment relationships and their relevance to habitat use, there are other interdisciplinary collaborations that hold great promise for addressing applied ecological, management-oriented, and socioeconomic problems that face fisheries science (*sensu* Schreck and Scanlon 1977). In the following sections, we briefly describe several emerging applications that demonstrate successful collaboration between fish physiologists and fisheries biologists that we deem to be especially promising.

Conservation physiology

Conservation physiology is a recently defined and rapidly growing field that applies physiological concepts and techniques to characterize and protect biological diversity. It seeks to understand and predict how organisms, populations, and ecosystems might respond to environmental variation and human activities, and thus to develop and evaluate conservation strategies (Cooke et al. 2013). Effective conservation physiology requires repeatable, often minimally invasive, and cost-effective techniques that are both physiologically and ecologically relevant. It also requires techniques that: (1) provide insights into physiological diversity; (2) identify critical habitats, variations in habitats, as well as their quality, and sources and consequences of stressors; (3) define the implications of environmental and anthropogenic

habitat change; (4) identify and elucidate the reproductive mechanisms and their implications for demographic processes; and (5) evaluate the efficacy of conservation-oriented management strategies (Cooke and O'Connor 2010; Cooke et al. 2013). Cooke and O'Connor (2010) provide a summary of the constraints and challenges that presently limit the ability of conservation physiology to generate, translate, and/or contextualize actionable information that could be used by managers and policy-makers. Our hope is that (via interdisciplinary efforts) fish physiologists, fish ecologists, fishery biologists, managers, and socioeconomists can work across the scales of Fig. 1 to both direct and be directed by the types of research needed to support effective management of species and their ecosystems.

Capture and release in commercial and recreational fisheries

Physiology continues to provide insights into the effects of capture and subsequent release (e.g., Moyes et al. 2006; Skomal 2007; Cooke et al. 2012b; Marshall et al. 2012), and enhance techniques to improve the welfare of fishes and other vertebrates released from commercial gillnets, trawls, and longlines (Farrell et al. 2001; Brill et al. 2009; Mandelman and Farrington 2007) and recreational fishing gear (Cooke and Schramm 2007). Fitness consequences ranging from stress (Kneebone et al. 2013), to physical or physiological injury (Pranovi et al. 2001), to mortality (Kaiser and Spencer 1995) may result from: encounter with the gear (which may result in catch or escapement), capture by the fishing gear, landing of the catch onto a vessel, and exposure on deck during catch-sorting operations (Ingolfsson et al. 2007; Giomi et al. 2008). Stressors may range from sublethal (but with consequences to growth or reproduction) to lethal, and mortality may be immediate or occur hours to weeks after the capture event (Raby et al. 2012). Several indicators of fish release condition are used by physiologists and fisheries scientists. Physiological tools following a capture event focus on perturbations to homeostasis reflected in blood or muscle parameters (e.g., Wood et al. 1983; Wells and Davie 1985; Brill et al. 2008a; Frick et al. 2009; Mandelman and Skomal 2009; Marshall et al. 2012), and common behavioral measures include condition assessment (Kerstetter et al. 2003) and/or rapid assays of reflex impairment as

indicators of survival potential (Davis 2002; Davis and Ottmar 2006). Particularly exciting applications combine these two approaches, iteratively groundtruthing laboratory assays with rapid field-based measures or telemetric technologies. Specifically, understanding physiological techniques can be used to identify handling procedures that reduce sublethal stresses and/or avoid lethal outcomes (Cooke et al. 2002; Suski et al. 2007; Mandelman and Skomal 2009), and also provide an understanding of the bioenergetics and other fitness consequences of capture (Meka and Margraf 2007; Brill et al. 2008b; Musyl et al. 2011).

We argue that many studies have fallen victim to the pervasive fallacy that physiological perturbations are proportional simply to the duration of exertion (and absent a measure of its intensity) by overlooking the fundamental relationships between drag, metabolism, and endurance, as they relate to captured fish. As shown in Fig. 5 (redrawn from Videler 1993), drag (D) on a moving object is proportional to kinematic viscosity of the fluid (Δ_w), wetted surface area (A_w), the coefficient of drag (C_{dw}), and the square of velocity (U). The coefficient of drag is a function of body shape, and therefore is the factor upon which natural selection can operate (i.e., more streamlined fishes have lower C_{dw}). Note, however, that drag is primarily influenced by velocity and that the exponential increase in drag with velocity is independent of C_{dw} , even though fishes such as tunas with streamlined body shapes (i.e., a low C_{dw}) experience a lower value of drag at equivalent swimming speeds (Fig. 5a). The net result of the exponential relationship of drag and velocity is a roughly similar exponential increase in metabolic rate with increases in swimming speed, which inescapably means the power demand required to overcome drag at high velocities must be met anaerobically. The fundamental relationship of an exponential increase in power demand with velocity results in the exponential decrease of endurance with swimming speed (Fig. 5b). In other words, fishes cannot sustain maximum speeds (U_{burst}) for more than a fraction of a minute due to the rapid depletion of muscle glycogen and its conversion to lactate (i.e., due to the oxygen debt incurred during high-speed swimming; Beamish 1978). Fishes are thus essentially two-gear animals, cruising aerobically at low speed (U_{sust}), but capable of vigorous but short anaerobic sprints to capture prey and avoid predators (Videler and Weihs 1982). During capture, fishes can only exert maximal

effort for very short periods (i.e., a fraction of a minute; Fig. 5b). In brief, both biochemistry and physics require that if effort is maximal, it cannot be sustained because of the exponential relationship of speed and drag. Therefore trying to correlate blood perturbations with “fight time,” without considering the intensity of activity, is based on flawed logic and is a major reason why the data obtained from this approach often resemble a shotgun-pattern relationship when “fight time” is plotted against various blood parameters (e.g., Kneebone et al. 2013). The flawed logic leaves much of the causal factors for variability unexplained, reducing the power of one variable to explain the other. The recent advent of relatively small recording tri-axial accelerometers (and other biologing and telemetric techniques; Brownscombe et al. 2013) has great potential to provide a quantitative measure of the intensity of activity during a capture event. When combined with a measure of fight time, these data should significantly improve investigations of the physiological disturbances associated with catch-and-release physiology and the prediction of post-release mortality rates.

More recent investigations of post-release survival have integrated the disciplines of molecular biology, telemetry, behavior, and population modeling for far more robust inferences (Moyes et al. 2006; Davie and Kopf 2006; Musyl et al. 2011; Cooke et al. 2012b). A better understanding of stress physiology can thus inform fisheries management and educate stakeholders about angling and handling best practices (Cooke and Schramm 2007; Pelletier et al. 2007; Shultz et al. 2011). For example, a field telemetry study revealed that bonefish (*Albula vulpes*) post-release angling mortality can be high ($\approx 40\%$) if predators are abundant (Cooke and Philipp 2004). Another study revealed that loss of equilibrium (even if regained prior to release) made fish six times more likely to be attacked by predators (Danylchuk et al. 2007). Laboratory studies that measured various blood parameters and reflex indicators revealed thresholds for air exposure and handling (Suski et al. 2007; Cooke et al. 2008), which informed the development of best handling practices specific to bonefish. Some anglers were also recovering bonefish in hyperoxic livewells with the assumption that it would assist recovery, yet physiological experiments revealed that providing fish with normal oxygen levels (normoxia) was preferable (Shultz et al. 2011). In this example, field observations

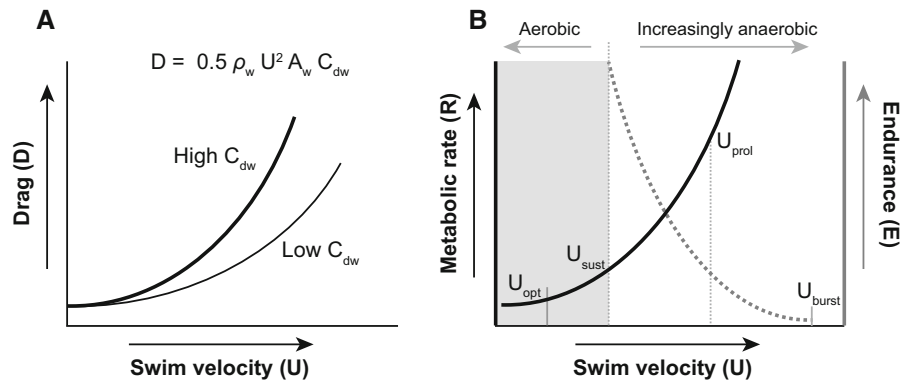


Fig. 5 Theoretical links between drag (D), swim velocity (U), metabolic rate (R) and endurance (E) in fishes released from hook and line. **a** The relationship between D and U for different drag coefficients (C_{dw}). D is a function of the density of the fluid (ρ_w), the U and surface area of the fish (A_w), as well as the species' C_{dw} . R increases with the square of U. Behavioral feedbacks (including streamlining and gait changes) in fishes minimize C_{dw} within physical and physiological bounds imposed by selection pressures acting on the species. **b** The relationships between R (black solid line; left y axis) and E (grey dashed line, right y axis) as a function of U. Optimal (U_{opt}) and maximum sustainable (U_{sust}) velocities are aerobic processes (grey box) that recruit mostly red muscle fibers and can be

maintained for long durations. U above U_{sust} requires increasing recruitment of white muscles and anaerobic conversion of glycogen to lactate. E falls as the square or the cube of U; from less than a minute at the maximum prolonged swim velocity (U_{prol}) to seconds at maximum burst speed (U_{burst}). Fishes must thus cycle effort by frequently reducing U to reduce R and recover E during prolonged exertion. The inverse relationship between M and E over U, when combined with effort cycling as well as gait and streamlining changes by the fish during hook and line capture, demonstrate the fallacy of assuming exhaustion is proportional to the duration of exertion absent a measure of intensity of the fish's activity. Adapted from Videler (1993)

identified a problem while experimental field and laboratory studies identified the mechanistic basis for mortality and revealed science-based opportunities for reducing it. Physiology is the perfect tool for identifying thresholds and testing various mortality-reducing strategies. Although the physiological response of individual fish to a capture event is probably of little concern to a fisheries manager, identifying problems and solutions of relevance to the population level through mechanistic physiological studies is certainly laudable. Continued human use of fish stocks for sustenance and recreation, coupled with ongoing diversification of technologies and techniques, render the field of stress physiology an interdisciplinary hotspot uniting fish physiology and fisheries science.

Fishing gear vulnerability and bycatch reduction

Fishing gear interactions, alternative baits, and bycatch reduction represent an exciting applied interdisciplinary forum for collaboration between physiologists and fisheries scientists. From the standpoint of conservation, enhancing the attractiveness or performance of gear relative to target species may change target:non-target catch ratios, but not the magnitudes of discards

or bycatch, thus rendering it an ineffective conservation strategy for fisheries that interact with species of concern. To avoid overly conservative management measures that function by keeping gear away from the bycatch species (e.g., time-area closures), an equally effective but more economical and desired alternative involves just the opposite, improving selectivity by keeping the non-target species away from fishing gear. Such an approach requires exploitable physiological and behavioral differences between target and non-target species that allow gear modifications to deter the latter but not the former, lest target catches decline (Southwood et al. 2008; Brill et al. 2009; Wang et al. 2010). Understanding the sensory abilities of fisheries resources (e.g., Horodysky et al. 2008a, b) and bycatch species is the critical first step to develop potential technologies (Southwood et al. 2008; Martin and Crawford 2015); these can then be tested with field gear modification trials and generate new hypotheses that can be addressed in the laboratory (Brill et al. 2009; Mooney et al. 2007). Similar strategies have been used to test synthetic alternatives to the use of species of concern as bait (e.g., Magel et al. 2007). The laboratory experiments and field testing processes iterate until successful deterrents and bait alternatives can be

developed, commercialized, and eventually mandated. Effective deterrents, attractants, and bait alternatives must be: (1) easy and safe to use; (2) affordable and exportable on a commercial scale; (3) reproducible over a wide range of environmental conditions; and (4) effective at their intended use with minimal reduction in the catch. Similar concepts apply to the development of fish deterrents from man-made structures (Welton et al. 2002).

Likewise, understanding how fisheries resources interact with gear over different environmental conditions has long been recognized as essential to the development of effective fishing strategies and for robust population assessments (e.g., Glass and Wardle 1995; Bigelow and Maunder 2007; Olla et al. 2000; Kotwicki et al. 2009), and this is especially so for highly mobile pelagic species such as tunas and billfishes (Brill and Lutcavage 2001; Lynch et al. 2012; Braun et al. 2015). The relationships of pelagic fishes to temperature and oxygen profiles of the water column are a classic form-function-environment example of the inferences possible when physiology and fisheries scientists unite. Some tuna and billfish species are generally limited to the warm oxygenated waters above the thermocline (from sea surface temperature to 8 °C less than sea surface temperature) because of the effects of temperature on cardiac function and the effects of ambient oxygen on metabolism; deeper-dwelling tuna species and swordfish compensate for life histories expressed in cooler, low-oxygen subthermocline waters via specific physiological adaptations primarily in the cardiorespiratory system (Brill et al. 1998; Lowe et al. 2000; Bernal et al. 2009; Galli et al. 2009). In regions with shallow thermo- and oxyclines, the catchability of epipelagic bycatch fishes can be extremely high (e.g., risk of hyperstability) in shallow sets targeting yellowfin tuna, and very low (e.g., risk of hyperdepletion) in deeper sets targeting swordfish and bigeye tuna because the physiology of these epipelagic bycatch species constrains them to concentrate in warm (in this case, shallow) waters (Brill 1994; Prince et al. 2010). The converse may be true in regions with deeper thermo- and oxyclines. As stock assessments of pelagic fishes typically use fishery-dependent catch per unit effort (CPUE) indices to estimate abundance, accurate population estimates require a better mechanistic understanding of the environment-fish-gear relationship across the landscape of species, gears, and spatiotemporal considerations.

Climate change

Predicted increases in global temperatures (1.4–5.8 °C over the next century) will likely have profound effects on the structure and function of aquatic ecosystems and fisheries worldwide (IPCC 2001; Perry et al. 2005). Such effects include, but are not limited to: (1) reductions in individual performance as oxygen and capacity-limited thermal tolerances are exceeded (Pörtner and Farrell 2008; Clark et al. 2013); (2) changes in phenology and physiology (Roessig et al. 2004); (3) shifts in the range and distribution of species (Perry et al. 2005); (4) changes in the composition of and interactions within communities and populations (Walther et al. 2002; Brander 2010); (5) changes in the productivity of fisheries stocks and ecosystems (Brander 2007; Cheung et al. 2010; Pörtner and Peck 2010); and (6) socioeconomic disruptions to fishing nations (Allison et al. 2009). Much of our understanding of the current and future effects of climate change on organisms comes from correlative or multivariate meta-analyses that demonstrate patterns over broad scales of geography (e.g., Parmesan 2006). These studies generally invoke the “black boxes” of climatic indices with little mechanistic insight at the organismal level (Helmuth 2009), and heuristically connect observed organismal patterns to changes in the local environmental conditions that presumably act on the collective physiological systems of the species studied. These approaches are good at detecting patterns, but their predictive ability to forecast future changes can be quite poor (Helmuth et al. 2005). Moreover, inferences from correlative or associative techniques are based on observations of realized rather than fundamental niches of the organisms in question, and the danger in predictive modeling from such baseline data centers on inattention to the specific mechanistic drivers acting on individuals of a given species (Kearney 2006; Helmuth 2009).

Changes in environmental conditions can influence the physiological performance of organisms by leading to rapid adjustments in physiological state at the individual level, variations in phenotypic plasticity that convey a fitness advantage at the individual or population level, and genetic adaptation to conditions at the population level (Helmuth et al. 2005). If changes are small, organisms may adapt rapidly. If changes are more pronounced, natural selection will favor those genotypes/phenotypes with better fitness

under those altered conditions; if changes are severe, organism will emigrate or perish (Helmuth et al. 2005). It is thus imperative to understand the directive selection of the changing environmental variable in question on an individual species, as well as the roles and rates of acclimation and adaptation in driving physiological responses (Helmuth 2009). The effects of climate change on a species depend on the extent of physiological and phenotypic plasticity of its environmental responses, the rate of evolution of these versus the rate of environmental change, and the nature and form of spatial variations in these parameters across the species' range (Chown and Gaston 2008). This is especially important to resolve for highly-exploited species, as overexploitation selects for a different suite of life history parameters and can substantially reduce the range of intraspecific physiological phenotypic niche space (Kuparinen and Merila 2007). It is impossible to predict the level of risk to which a fish is subjected without isolating and quantifying the magnitude of the environmental stressor and the ability of the organism to endure, resist, or avoid it (Helmuth et al. 2005). Understanding the physiological mechanisms that underlie how specific changes to environmental conditions affect all life history stages of fisheries resources is critical for predicting their ecological responses to climate change (Roessig et al. 2004; Helmuth et al. 2005). It is especially important to integrate physiological perspectives over the life cycle to predict climate change impacts on endemic fishes, those with life history stages with specific habitat requirements, and species with complex life history variation (Covich et al. 1997; Petitgas et al. 2013).

The fusion of physiological techniques with climatic, biogeographic, and ecological perspectives, and the advent of new field-based techniques, biophysical approaches, and quantitative methods, offer an unprecedented opportunity to generate, test, and evaluate interdisciplinary hypotheses on the effects of climate change (Helmuth et al. 2005). In particular, synoptic quantitative approaches including bio-climate modeling, DEB models, and particularly Species Distribution Models that link environmental variation to physiological processes and fitness over entire fish life cycles and over broad geographic landscapes have the potential to dramatically refine predictions of biomass and range expansion of fisheries resources under a changing climate if parameterized with the

appropriate mechanistic data (Jeschke and Strayer 2008; Araújo and Peterson 2012). Additionally, landscape-scale investigations of physiological traits and their ecological implications over broad spatiotemporal regions may disentangle both the mechanistic drivers of, and organismal responses to, environmental change over a wide variety of flora and fauna (Chown et al. 2004; Kearney and Porter 2009), including fishes (Hare et al. 2010). Ultimately, integrative systems-based approaches that elucidate the mechanistic roles of environmental and physiological variability in shaping behavioral responses offer predictive capacity to resource managers and policy makers involved in mitigating the adverse societal effects of natural and anthropogenic climate change (see Helmuth 2009).

Summary and conclusions: a plea for the sum of the parts

Fishes face complex environmental and anthropogenic stressors that have, in decades, fundamentally altered ecosystems properties that have evolved over millennia or longer (Fig. 6). Despite the obvious social, political, and economic implications of these changes, there remain many unknowns and no “magic-bullet” solutions (Pitcher and Lam 2010). Given an uncertain future of environmental change, there is much to learn about the mechanistic ecological and demographic relationships of fishes with the environment, as well as their interactions with humans and fishing gear. The integration of physiological knowledge into ecological and population assessment models can improve their predictions both with respect to responses to environmental change and alternative management plans and harvest strategies, and ultimately provide better tools to support management decisions and interventions (Cooke et al. 2013). In the interests of conservation and stewardship of aquatic resources, we must integrate physiology into fisheries management and restoration plans (Cooke and Suski 2008; Cooke and O'Connor 2010).

Historically, the disciplines of fish physiology and fisheries biology have functioned largely in isolation, where specialists in the disciplines have conducted “stove-piped” research. The disciplines have only occasionally interacted synergistically in a multidisciplinary context, with sporadic exchange of ideas outside of annual conferences (Cooke et al. 2008). We

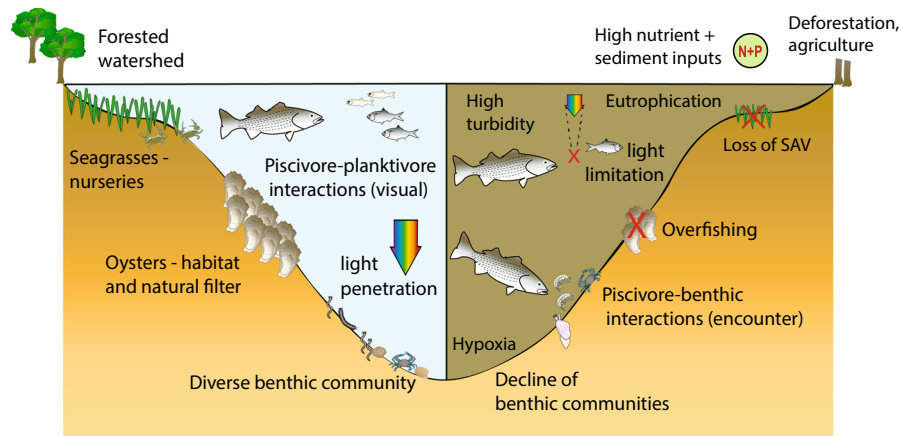


Fig. 6 Rapid, multifocal, and complex effects of anthropogenic influences and climate change on fisheries resources and ecosystems using Chesapeake Bay as an example. Over the past 250 years, the Chesapeake Bay watershed has experienced dramatic increases in land use, human population growth, and fisheries exploitation (Jackson et al. 2001). The combined effects of high nutrient and sediment inputs, eutrophication, and overfishing have led to extensive seasonal hypoxia, increased turbidity, decline of submerged aquatic vegetation, and diseases in fisheries resources (Kemp et al. 2005). Reductions in water

quality can directly affect fisheries resources by limiting growth (mechanisms: diet, oxygen, temperature, disease), immunocompetency (diet, oxygen, temperature, disease), and/or disrupting ecological energetics and biodiversity (diet, disease, predator-prey interactions) (Scott and Sloman 2004). Understanding these complex problems requires an interdisciplinary research approach focused on developing robust cause-effect relationships by integrating laboratory, behavioral, and field perspectives

contend, as have others, that fish physiology, fisheries science, and resource management should optimally function in a collaboratively iterative interdisciplinary context, with equal voice in identifying, planning, and evaluating future research directions and their products (e.g., Brill 1994; Brill and Lutcavage 2001; Cooke et al. 2008, 2013). This synthesis is therefore a plea for “sum of the parts”, where each discipline develops hypotheses that can be tested by the other in an integrated iterative process, with the goal of transdisciplinary gains that push both disciplines to accomplish more than either can alone (Maguire et al. 1994; Cooke et al. 2008). Long-held disciplinary Rubicons must be crossed to facilitate this dialogue and collaboration: physiologists must be willing to give up some measure of control on sources of variability and apply new tools and techniques to move beyond simple reductionist experimental settings to the multivariate conditions experienced by wild fishes, and ecologists and applied fisheries scientists must resist the siren song of correlation and create and apply tools that explain and realistically connect individual mechanistic responses to environmental variation to population and ecosystem level outcomes and consequences. The resulting science

provides far more hope for synoptic insights into current fisheries issues than the status quo of isolated research programs with rare intellectual cross-fertilization that may result from the disconnect between graduate training philosophies and funding opportunities that typically favor short-term, dimension-reducing, individual-based insights in physiology versus longer term, multivariate, ecosystem-based insights in ecology.

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