

FIELD PHYSIOLOGY: Physiological Insights from Animals in Nature

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■ **Abstract** Whereas comparative physiology documents the range of physiological variation across a range of organisms, field physiology provides insight into the actual mechanisms an organism employs to maintain homeostasis in its everyday life. This requires an understanding of an organism's natural history and is prerequisite to developing hypotheses about physiological mechanisms. This review focuses on a few areas of field physiology that exemplify how the underlying physiology could not have been understood without appropriate field measurements. The examples we have chosen highlight the methods and inference afforded by an application of this physiological analysis to organismal function in nature, often in extreme environments. The specific areas examined are diving physiology, the thermal physiology of large endothermic fishes, reproductive physiology of air breathing vertebrates, and endocrine physiology of reproductive homeostasis. These areas form a bridge from physiological ecology to evolutionary ecology.

All our examples revolve around the central issue of physiological limits as they apply to organismal homeostasis. We view this theme as the cornerstone of physiological analysis and supply a number of paradigms on homeostasis that have been tested in the context of field physiology.

INTRODUCTION

As a discipline, physiology examines the mechanisms by which an organism maintains homeostasis. The broad field of comparative physiology is centered on adaptive physiological variation among species from different environments. Field physiology goes one step further, by measuring, with a wide spectrum of techniques, the mechanisms employed by organisms to carry out their functions under actual environmental conditions. Therefore, by extension, field physiology is the examination of homeostatic mechanisms in the field. While we often find examples of wonderful physiological mechanisms to maintain homeostasis in extreme environments, there are also excellent examples where the organism simply

avoids the extremes by behavioral or other nonphysiological processes. For instance, small organisms take advantage of microhabitats that enable them to avoid environmental extremes. Many desert rodents avoid the daytime heat by being active at night when temperatures are moderate and remain in their burrows during the heat of day. In contrast, large mammals such as the oryx or the camel are too large and cannot escape the desert heat and thus have developed a series of well-documented physiological and anatomical adaptations to these extreme temperatures (1, 2).

A cornerstone of field physiology is an appreciation for and understanding of the natural environment and its associated history. Natural history provides a basis to develop hypotheses and questions about what physiological problems confront animals in the field and, therefore, what mechanisms an animal might require to survive (2–4). One of the innovations in recent years concerns the quantification of natural history (5) and, specifically, of the role of natural selection in shaping the evolution of physiological traits (6, 7).

Some of the earliest and best-known examples of physiology in the field started with a series of simple observations of an organism in its environment. For example, field work in the California deserts and associated observations of kangaroo rats led Schmidt-Nielsen and colleagues to ask how these animals deal with the xeric desert environment (2). Where do they get their water? Is their kidney different from other mammals? Similarly, observations of marine mammals led Scholander and Irving et al. to ask how these animals remain submerged for such prolonged periods of time (8). Do they drink sea water? Do they have an extrarenal salt gland like seabirds, or do they have a specialized kidney (9)? All these early and fundamental studies in comparative physiology started with observations of animals in their natural environment. Even though researchers made their initial observations in the field in these early studies, they almost always brought animals into the laboratory to investigate their physiology. This was because laboratory investigation was not only the obvious solution to the problem, but in many cases it was the only way possible because the available equipment was large, cumbersome, and not suitable for field use.

Nonetheless, laboratory investigation offers a precision not always possible in the field, even with the advantages of modern technology. In the laboratory, an investigator can hold all variables constant except those that are of interest. In contrast, it is difficult to control the variability in both biotic and abiotic features of the natural environment. A well-designed field study accepts the variability of the natural environment but works to insure that the variation between control and experimental groups is the same. Thus we try to create a situation where the role or impact of natural variation is reduced or at least accounted for. Finally, the issue is not whether field versus laboratory investigations are better, but how to achieve the optimum mix between both.

It would be unrealistic to review the whole range of physiological investigations that have been carried out in the field. Therefore, this review focuses on a few areas of field physiology that exemplify how the underlying physiology could not have been understood without appropriate field measurements. Notably, exploring the

limits of physiological systems has been a hallmark of physiological analysis since the Krogh principle was first presented (10). The examples we have chosen highlight the methods and inference afforded by an application of this physiological analysis of extreme environments in the natural realm. Furthermore, the areas that we examine, diving physiology, the thermal physiology of large endothermic fishes, reproductive physiology of air-breathing vertebrates, and endocrine physiology of reproductive homeostasis, also bridge from the field of physiological ecology to evolutionary ecology.

In choosing these examples, we highlight the two conceptual frameworks that have served to focus our perspective on physiological processes in nature: the comparative approach applied to populations and species, and the individual approach applied to differences among individuals within a population (11). Each of these levels of biological analysis has strengths and weaknesses. For instance, the individual approach largely ignores the large-scale physiological differentiation observed at high levels of taxonomic diversity, which is the endpoint of adaptational processes (12). However, the individual approach excels at highlighting the evolutionary factors responsible for divergence in physiology at these higher levels—natural selection underlies the process of adaptation. It is also possible to carry out fine-scale analysis of causation with manipulations of physiology or those individual traits that result from physiological process. When homeostatic mechanisms fail, the outcome is invariably death. Thus differential survival or reproduction as a function of variation in organismal homeostasis among individuals is the mechanism by which physiology evolves.

In contrast, the comparative approach has classically been applied to the analysis of physiology in extreme environments and has identified those species in extreme environments that have, in some ways, extraordinary adaptations of physiology. Presumably, these species are near the functional and genetic constraints imposed on adaptational processes. Allometry is a field of study in physiological analysis that has provided a classic treatment of constraints on adaptation. Although useful in identifying such functional limits, differences in environment confound the analysis as do those biases inherent in a strictly phylogenetic analysis (12). Rarely are both approaches to the analysis of physiology in natural systems combined. We highlight a few studies that are exemplary in this regard. We do not, however, supply a comprehensive review of the evidence for these paradigms, as these have been developed over the decades in laboratory settings. Where appropriate, we supply a number of in-depth review citations to these laboratory-developed models and the extensions to a field setting.

DIVING PHYSIOLOGY

For millions of years a central component of the basic homeostatic machinery of air-breathing vertebrates has been just that, reliable access to air. The physiology of diving vertebrates is built around an enhanced capacity to function in the absence of

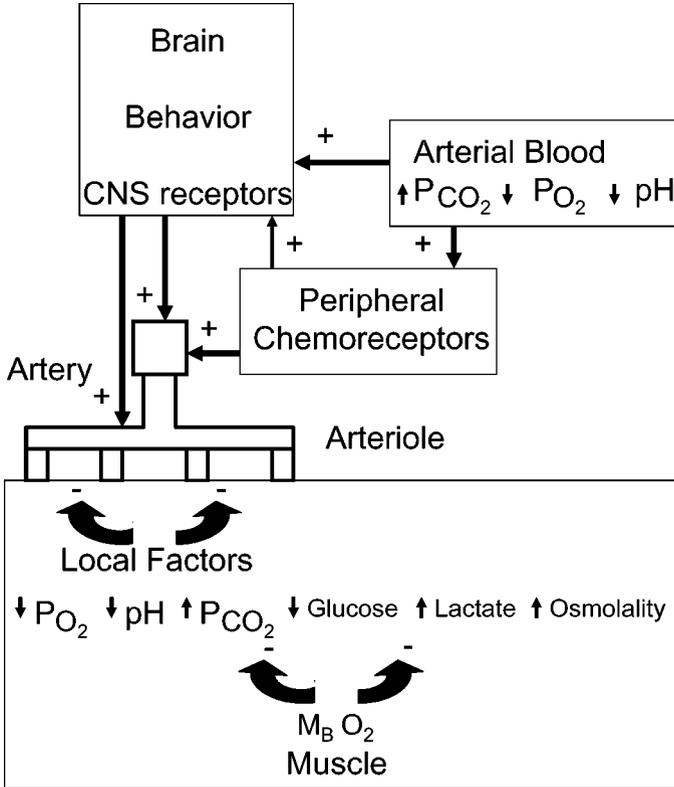


Figure 1 Proposed control of blood flow and O₂ delivery to muscle that regulates the transition from aerobic to anaerobic metabolism in a diving seal (13).

oxygen, and is marked by the tolerance by divers of considerable variation in tissue O₂, CO₂, and pH. The ability to modify or override normal control mechanisms has allowed diving reptiles, birds, and mammals to successfully invade and exploit the aquatic environment (Figure 1). The problems faced by diving vertebrates can be divided into adaptations that deal with pressure and adaptations to prolong their ability to remain submerged. Adaptations to pressure include mechanical effects of pressure, as well as the problems coupled with increased solubility and, in some cases, toxicity of N₂ and O₂ at high pressure. Adaptations to prolonged time spent underwater are linked to oxygen stores, how fast they are used, and whether there is any need for anaerobic metabolism. Given the difficulties of carrying out studies under high pressure, it is not surprising that the majority of research on diving has centered on metabolic processes during a dive. This review concentrates on field studies that have increased our understanding of diving physiology, a broader

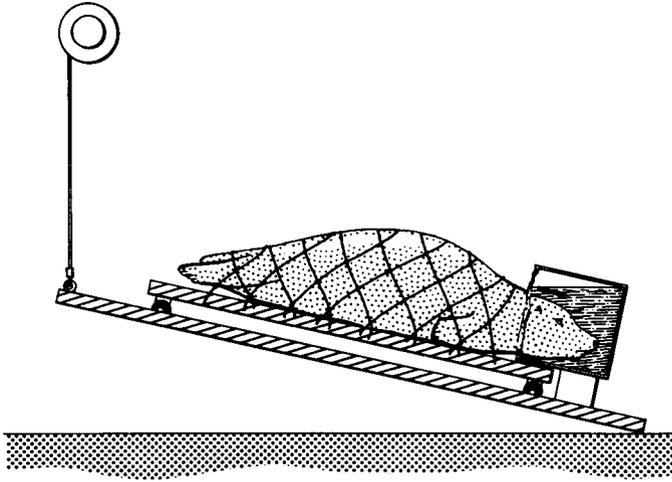


Figure 2 An example of the early experimental apparatus for experiments used a forced-dive approach (20).

appreciation of this activity can be obtained from a number of excellent reviews (13–15a).

Pioneering studies of the dive response and diving metabolism of mammals and birds were for years carried out almost exclusively in a laboratory setting (Figure 2). The early work of Scholander and Irving showed that when a captive mammal or bird was forced to dive, there was an overall reduction in metabolism coupled with an increased reliance on anaerobic metabolism as indicated by a postdive release of lactic acid (Figure 3) (16–18). This dive response was initiated by a profound bradycardia with associated reductions in cardiac output and blood flow to peripheral tissues (19). Later work using labeled microspheres confirmed that blood flow was reduced to all major organ systems except the heart, lung, and brain (20). Although this pioneering work provided insight into the maximum physiological response of a diving mammal, its relevance to the natural setting was unclear. Even Scholander (17) warned that his laboratory measurements might not adequately describe the physiology of a freely diving animal. The tools and techniques were barely available for laboratory measurements let alone for studies of freely living animals. Further evidence that the maximum dive response observed in a laboratory might not occur in nature was uncovered by Elsner et al., who studied the dive response of captive trained or unrestrained aquatic mammals. Elsner et al. found that voluntarily diving subjects exhibited a significantly reduced bradycardia compared with forced dive animals (Figure 4) (21–24).

A major breakthrough in the study of diving physiology came when Kooyman capitalized on a novel situation in the Antarctic and literally took the laboratory

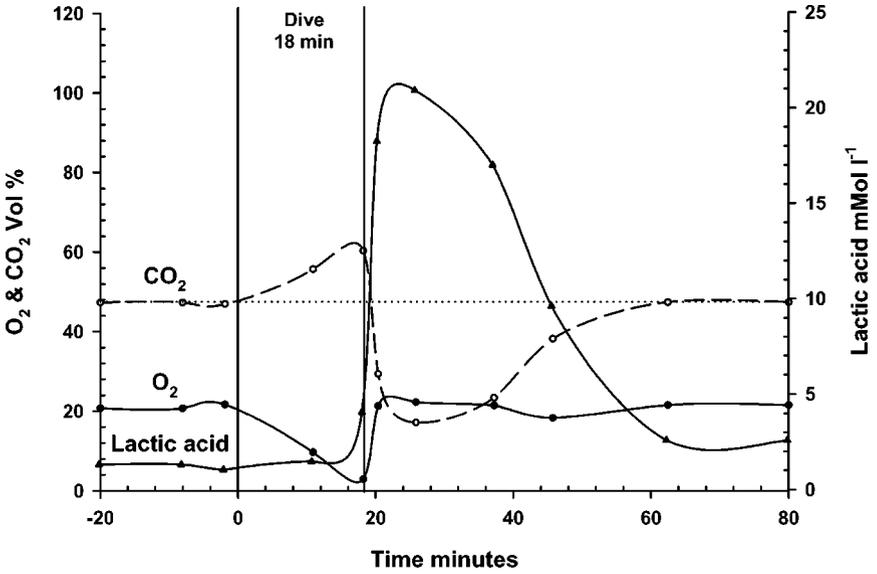


Figure 3 Effects of forced-dive submersion of a 42-kg gray seal, *Halichoerus grypus*, on arterial blood chemistry (17).

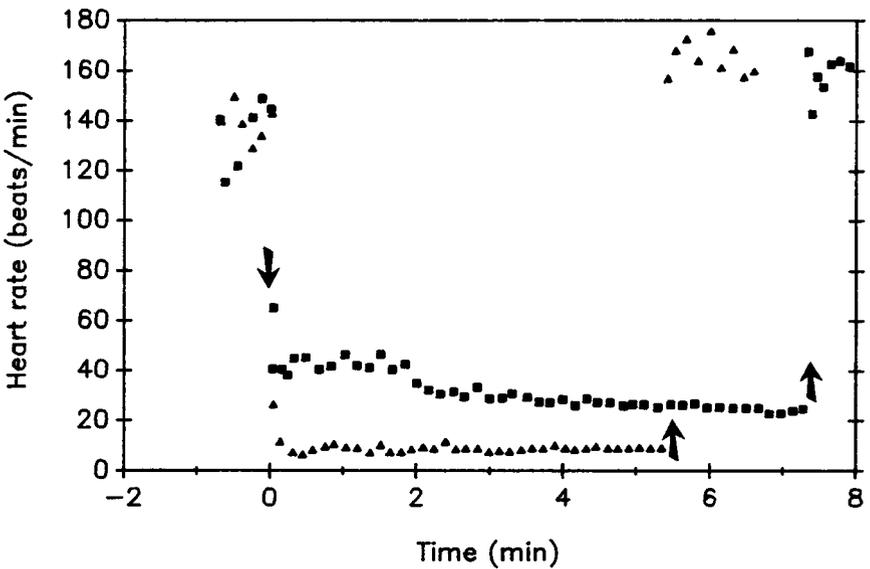


Figure 4 Heart rate in the harbor seal during trained head submersion (solid boxes) and forced submersion (solid triangles) (23).

into the field to study the diving behavior and physiology of freely diving Weddell seals, *Leptonychotes weddelli* (25). Weddell seals make a living diving in and around small openings in fast sea-ice, which is attached to the shore and in certain situations can cover the surface of the ocean for many kilometers. Because Weddell seals are adapted to living in this environment, they routinely breathe through small cracks or holes in the sea-ice. Kooyman exploited this natural ability to create a novel field laboratory. He moved a seal to an area where there was only a single sea-ice hole for many kilometers and thus created a situation where the animal had to return to the same location to breathe. Kooyman and colleagues then placed a small portable laboratory over this hole and measured the animal's pulmonary function, heart rate, and metabolic rate while the animal determined its own diving behavior (26–28). Similar to the work carried on captive unrestrained diving mammals, freely diving Weddell seals showed a moderate bradycardia. However, the degree of bradycardia increased in longer dives and was exhibited at the beginning of the dive. This indicated that the dive response varied in relation to the metabolic needs of the seal and that the seal knew whether it was going to make a long or short dive.

Although this work suggested that our understanding of the physiology of diving mammals was flawed, it was not until Kooyman's group was able to monitor blood lactic acid levels before and after a dive that they were able to show that Weddell seals dove aerobically during the majority of their dives (29, 30). This work showed that lactic acid levels remained constant for dives up to 20 min and thereafter rapidly increased with increasing dive durations (Figure 5). They concluded that animals could dive aerobically for dives lasting up to 20 min. This work defined the maximum time an animal could remain submerged without utilizing anaerobic metabolic pathways; the aerobic dive limit (ADL) was calculated as $ADL \text{ (min)} = \text{total oxygen store (ml O}_2\text{)}/\text{diving metabolic rate (ml O}_2\text{ min}^{-1}\text{)}$. An important observation was that when Weddell seals exceeded the aerobic threshold, the postdive surface interval increased disproportionately relative to dive duration (29, 30). The greater surface intervals were needed to clear the lactic acid that accumulated during the dive. One of the disadvantages of anaerobic metabolism during diving is that while a diver may increase the duration of a single dive, the total accumulated time spent underwater is reduced. This is because the animal must spend proportionately more time at the surface clearing lactic acid (13).

The tremendous potential of studying the physiology of freely diving Weddell seals in McMurdo Sound, Antarctica became apparent to other researchers as well. A variety of research teams have since used this field laboratory to examine renal function (31), lung collapse (32), blood gases and hematocrit variation (33, 34), substrate utilization (35), cardiovascular control (36), blood chemistry homeostasis during diving (37), diving metabolic rate (38), muscle and aortic temperature during diving (39), re-examination of aerobic dive limit (40), heart rate and body temperature variation, myoglobin saturation (41), hormonal control and splenic contraction (42, 43), hunting behavior (44), and locomotor mechanics (45).

While all of these studies incorporated new technologies and approaches to working with Weddell seals diving from a sea-ice hole, a few stand out for

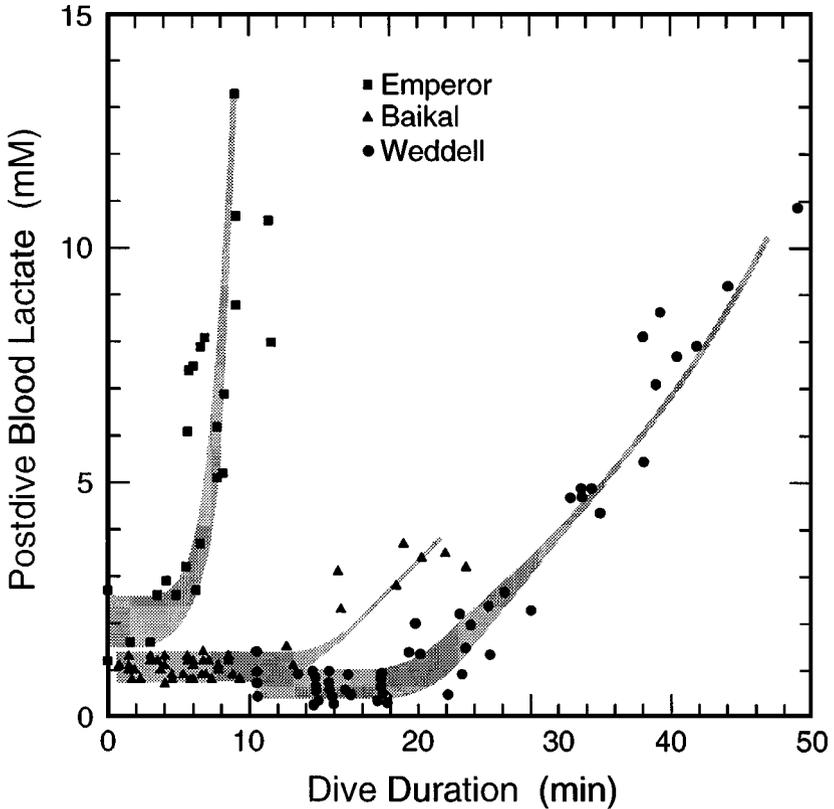


Figure 5 Postdiving blood lactate concentrations and diving durations of the emperor penguin, Baikal seal, and Weddell seal (15a).

incorporating truly innovative technology. A group led by Hochachka and Zapol enlisted the engineering expertise of Hill to develop a microprocessor-controlled system to periodically sample blood during the time the seal dove (35, 36). This technology was used to document when lung collapse occurred during a dive (32); changes in blood gases and hematocrit (33); substrate utilization, cardiovascular control, heart rate, and body temperature variation, myoglobin saturation (41); hormonal control, and splenic contraction (42, 43).

Although, lung collapse had been observed in simulated dives (46) and in a freely diving trained dolphin (47), it had never been quantified in a freely diving animal. The microcomputer-controlled blood sampling system provided confirmation of the functional importance of lung collapse in a freely diving seal (Figure 6) (32). Marine mammals have an advantage in that, unlike human divers, they exclusively breath-hold dive and thus carry only a limited amount of air in their lungs during a given dive. Deep-diving marine mammals avoid problems associated with

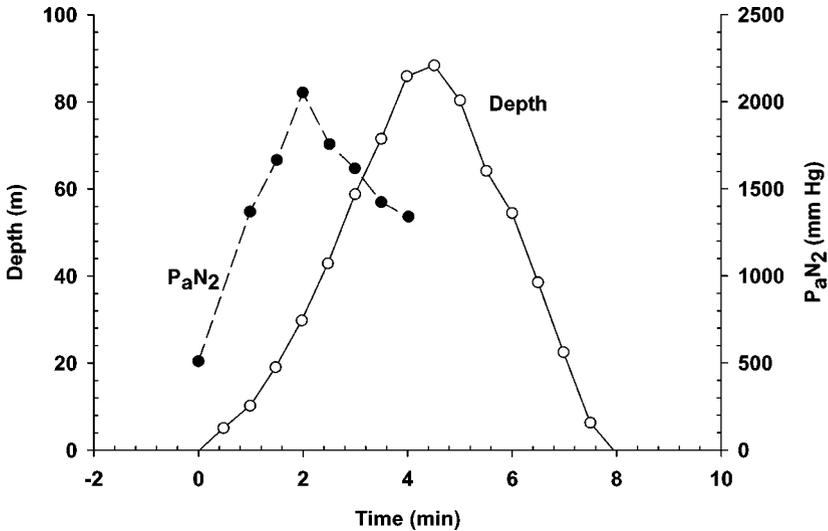


Figure 6 Depth of dive combined with serial determinations of P_aN_2 during dive. P_aN_2 values determined early during a dive when pulmonary gas exchange spaces are collapsing. Samples were collected every 30 s (32).

tissue N_2 accumulation by allowing their lungs to collapse during the initial period of the dive. As the lung collapses, air is expressed into the large bronchioles and trachea where gas uptake at elevated pressures cannot occur (13, 15a). Given that N_2 and O_2 tensions in the blood remain relatively low during the dive, nitrogen narcosis, decompression sickness, and oxygen toxicity are thought to be avoided. However, it is still unclear how penguins, small cetaceans, and sea lions avoid the bends because they can make many repetitive dives on a full lung and do not always undergo lung collapse (13, 15a, 47).

Although Weddell seals offer a truly exceptional system to study diving physiology, they represent but a single species in a very unusual situation. The only other diving animal that has been studied in this way is the emperor penguin (48). However, comparable results have been obtained in a few studies where aerobic dive limits have been measured using freely diving trained bottlenose dolphins, *Tursiops truncatus* (49), California sea lions, *Zalophus californianus* (50), Beluga whales, *Delphinapterus leucas* (51), and captive Baikal seals, *Phoca sibirica* (52). All these studies support the ADL model as originally proposed by Kooyman et al. (29).

One of the goals of field physiology is to understand when physiology limits behavior; therefore, it would be instructive to observe how often and under what conditions animals diving in nature stay within or exceed the ADL. Recent advances in technology have allowed simultaneous measurements of diving behavior and metabolic rate. These studies show that in certain situations diving animals may exceed their ADL, which implies the potential for anaerobic metabolism. For

example, Antarctic fur seals, *Arctocephalus gazella*, rarely exceed their cADL because they make short shallow dives feeding near the surface. In contrast, the cADL is routinely exceeded in long and/or deep diving Australian *Neophoca cinerea* and New Zealand, *Phocarctos hookeri* sea lions (Figure 7) (53). Animals that feed at or near the sea bottom consume large prey that may require prolonged durations to effectively capture (53–59).

Such measurements are not just of interest to physiologists, they also have relevance to wildlife managers. For example, it is important to know whether a species in decline is operating at or close to its maximum physiological capacity, because if so, it will be less capable of compensating for normal environmental- or human-caused changes in its environment. In contrast, an animal that is operating well within its physiological capacity will be more capable of responding to environmental fluctuations. Such animals would be able to draw on a greater physiological reserve and pursue prey deeper, or dive longer or forage for greater periods (53, 56). Over the past decade many fur seals' populations (South America fur seal, *Arctocephalus australis*; New Zealand fur seal, *A. forsteri*; and California sea lion, respectively) have experienced spectacular population growth that is in marked contrast to an apparent stability or even decline in all of the sea lions that feed on or near the bottom (Steller, *Eumatopias jubatus*; Australian; southern, *Otaria flavescens*; and New Zealand sea lion), many of which are sympatric with near-surface-feeding fur seals (56).

Studies of diving behavior would not have been possible without the amazing developments in digital electronics, which have provided field biologists with a new form of biotechnology that allows the study of complex behavior and physiology in freely ranging animals. This technology has produced data loggers small enough to be attached to animals while they freely go about their activities (Figure 8). Data from these tags are obtained when the tags are recovered (archival tags) or when transmitted via satellite (60, 61). These tags have been used extensively with marine mammals, fish, birds, and reptiles. Due to the large size and in some cases the ease of capture of marine mammals, the technology for attached instrumentation was initially developed for use with these animals and has been used to record the ambient acoustic environment (62–64), heart rate (65), ventilation rate (66), swim speed (58, 67, 68) and acceleration (69, 70).

Satellite tags are used when one cannot recover the data logger from the animal. A limitation of this technology is that the satellite transmitter must be out of the water to communicate with an orbiting satellite, therefore the technology has mainly been used on air-breathing vertebrates that surface regularly such as marine birds (71, 72), sea turtles (73), marine mammals (74, 75) and most recently sharks (61, 76). An example of the kind of data that can be acquired with this technology is shown in Figure 9.

Future Directions

A major area of research in diving physiology that could benefit from field measurements is how deep-diving marine mammals and birds handle the effects of

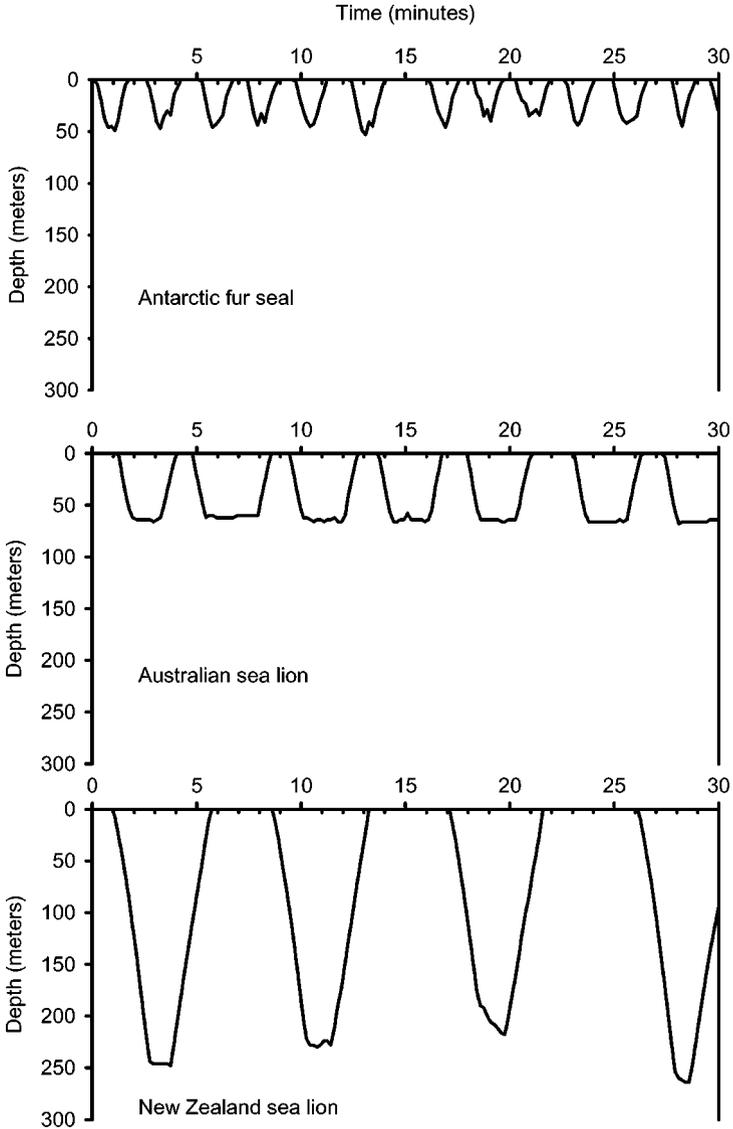


Figure 7 The diving pattern of Antarctic fur seal, *Arctocephalus gazella*, the Australian sea lion, *Neophoca cinerea*, and the New Zealand sea lion, *Phocartos hookeri*, are compared. All axes are expressed in the same absolute units to facilitate comparison. The two sea lions feed at or near the bottom, whereas the fur seal feeds near the sea surface (53).

pressure. There are two aspects to this work: those that focus on hydrostatic effects of pressure and those associated with effects of dissolved gases such as nitrogen. Specifically, are deep divers susceptible to high-pressure nervous syndrome? How do repetitively diving marine mammals and birds that do not go through lung collapse avoid decompression sickness (15a, 77)? Further examination of the role of physiology in determining the optimal diving pattern would also be a productive area of research, as the necessary technology currently exists.

ENDOTHERMIC FISHES

A major advantage of endothermy is the ability to occupy and travel between different thermal habitats, while critical organ system, such as the nervous system and aerobic muscles can be maintained within a narrow set of biochemically optimal temperatures (78). For example, marine mammals and sea birds can go from a warm tropical island or surface waters to cold, food-rich regions of the ocean, all the while keeping their core body temperatures high and constant. However, only 27 out of 25,000 species of fish and sharks have evolved some form of regional endothermy (79). As gill breathers, fishes cannot become true endotherms because water contains only 1/40th as much oxygen, although it conducts heat 25 times faster than air (79). As a result, blood passing through the gills always equilibrates with the ambient thermal environment. Thus the vast majority of fishes remain within 1 to 2°C of the ambient environment (79).

Nevertheless, regional endothermy has developed along two different paths: one typified by tunas and sharks that conserve metabolic heat in the muscle, viscera, and brain and one recently discovered in billfishes where only the cranial cavity is warmed (79, 80). Regardless, common prerequisites for regional endothermy are large body size, a heat source, and a vascular system (counter-current heat exchanger) to conserve the heat. The physiological, biochemical, and anatomical mechanisms of tuna endothermy have been well documented (79, 81–89). Thirteen species of Scombrid tunas and 5 species of lamnid sharks exhibit regional endothermy, in some cases maintaining internal temperatures an astounding 21°C above ambient (79, 80, 90–92). Elevated temperatures in tuna are maintained by the internal location of the red oxidative muscle coupled with a vascular supply that passes blood through a counter-current heat exchanger, allowing retention of heat produced by the red muscle. In billfish, the brain and eyes are kept up to 13°C above ambient by a novel heater organ derived from the skeletal muscle around the eyes (79).

Mapping the key features of endothermy on a molecular phylogeny of the teleost fishes indicates that endothermy evolved independently at least three times in the Scombrid tunas, whereas cranial heaters evolved at least twice in the billfishes (Figure 10) (93). These independent origins of endothermy suggest that this energetically expensive strategy was under strong selection. Furthermore, the three independent origins of endothermy correspond to the independent expansion of

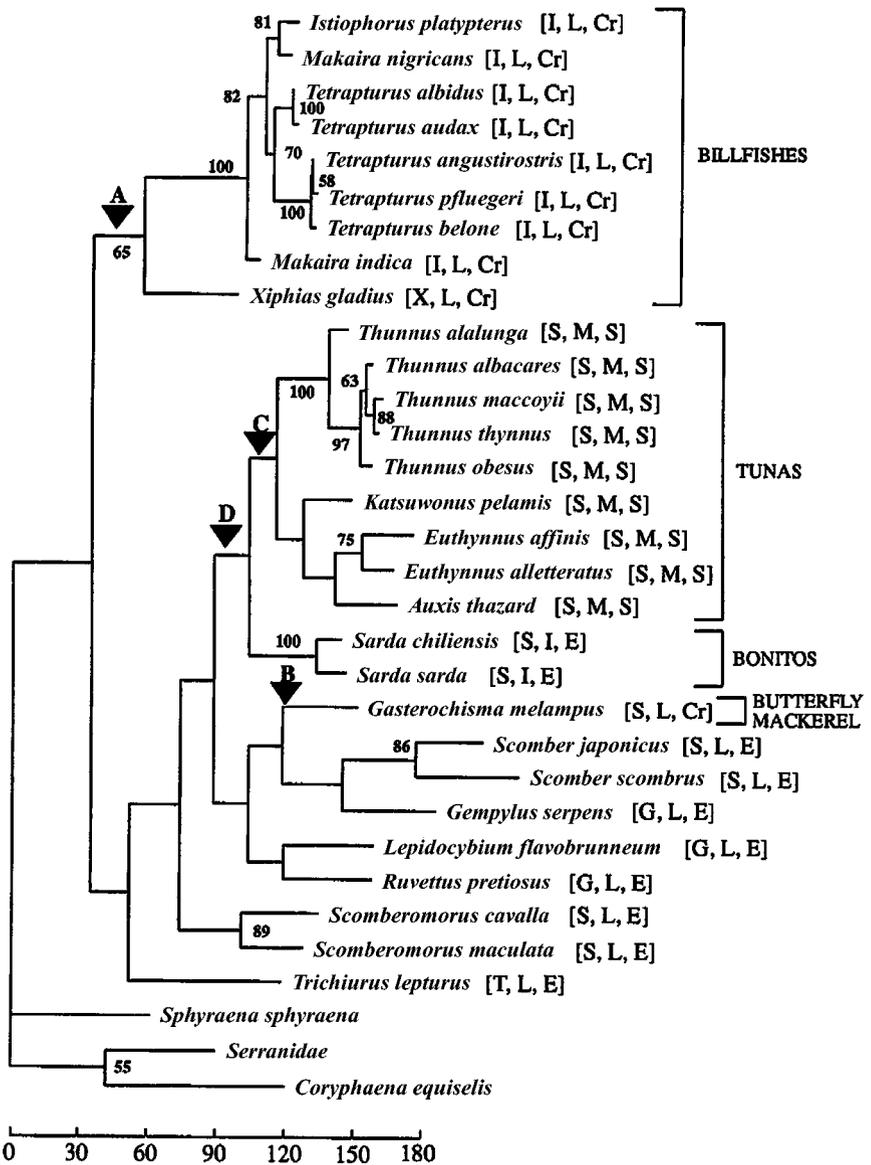


Figure 10 Phylogeny of the Scombroidei on the basis of a parsimony tree derived from a 600 base pair of cytochrome *b*. The arrows associated with specific nodes refer to (A) modification of the superior rectus muscle into a thermogenic organ, (B) modification of the lateral rectus muscle into a thermogenic organ, (C) systemic endothermy using vascular counter-current heat exchanges in the muscle, and (D) some internalization of red muscle along the horizontal septum (93).

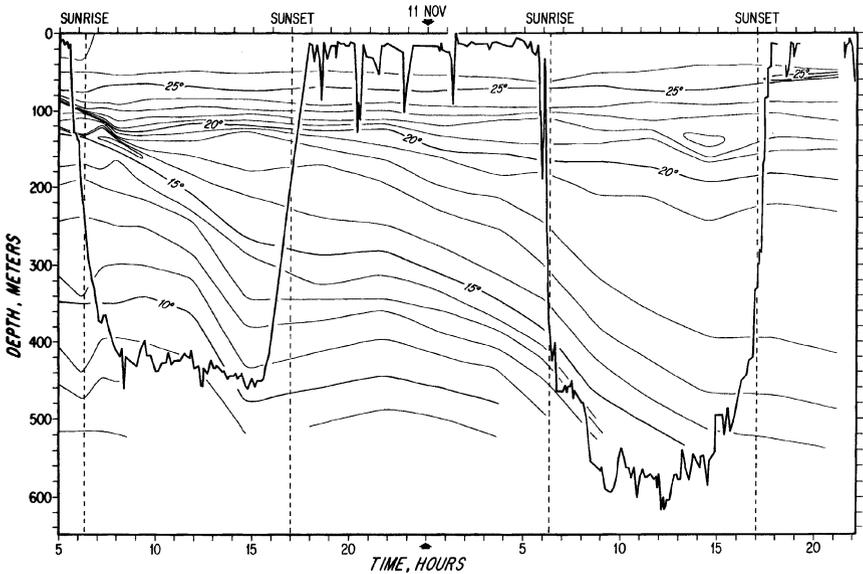


Figure 11 A depth record from a swordfish, *X. gladius*, illustrating their diurnal vertical migration. Swordfish pass through the thermocline and encounter large changes in the water temperature at dusk and at dawn. Data were derived via acoustic telemetry (94).

these three lineages into cool temperate waters. This analysis supports the role of fish endothermy as a physiological adaptation associated with niche expansion (93). However, an understanding of the importance of fish endothermy to niche expansion can be understood only by examination of the physiology of these fishes operating in nature.

Physiological measurements of freely ranging fishes were until recently carried out with acoustic tracking devices (61, 89, 94, 95). This was extremely difficult because it required real-time tracking by ship and thus tracks were limiting to just five or six days and only a single tagged animal could be followed. However, this technology provided the first real insight into the importance of regional endothermy to fishes in nature (Figure 11). For example, swordfish, *Xipias gladius*, spend the night in the warm surface waters (25°C), but during the day they vertically migrate to much deeper (400–600 m) and colder (8–9°C) waters (94). However, what is most impressive is that in spite of the large deviations in ambient temperature, the cranial temperature of the swordfish remains surprisingly constant (Figure 12).

More recently archival tags have been deployed on fishes and sharks, thereby allowing collection of data for greater time periods independent of a research vessel (61, 89). For use on fish, the archival tags are surgically implanted inside the peritoneal cavity. Pressure and internal temperature sensors are located within the body of the tag. A stalk protruding from the archival tag carries the light and water

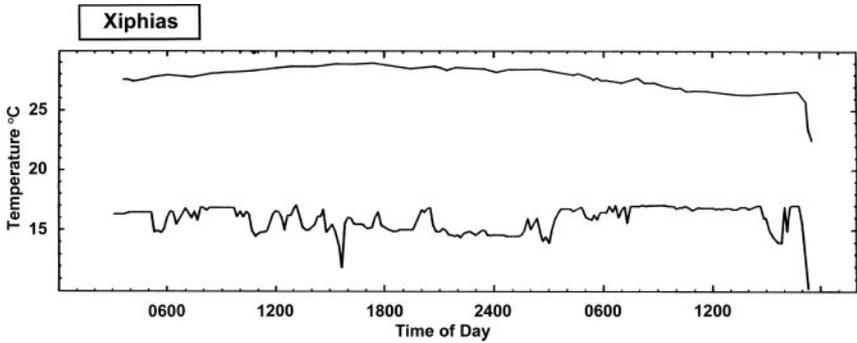


Figure 12 Temperature telemetry record from a swordfish, *X. gladius*, showing how effective the cranial heater is in keeping the brain temperature elevated and relatively constant (94).

temperature sensors externally. Data are stored in the tag until it is recovered, usually by fishermen. Information on the location, diving behavior, ambient, and internal temperature preferences can be obtained. To date blue fin tuna, *Thunnus thynnus*, have been tracked for 3.6 years (61, 89). Similarly, even though blue fin tuna repeatedly venture into cold waters, their internal body temperature remains relatively constant and elevated (Figure 13). Finally the critical role of large body size to regional endothermy can be seen in the greater thermal variability in a small tuna compared with a larger tuna of the same species (96) (Figure 14).

The phylogenetic analysis as used for billfish illustrates the power of the phylogenetic perspective in elucidating the origins of traits, whereas the detailed individual measurements on free-ranging fish with high-tech recording equipment provides crucial information on the actual natural history context that we noted above. More syntheses using both methods will be crucial in unraveling the origin of physiological adaptations and the environmental conditions that contributed to their evolution and maintenance. An emergent theme throughout this review is the profound role behavior has in shaping selection on physiological traits. In the case of billfish, maintenance of high cranial temperatures is thought to be the direct result of selection on the ability these fish to be effective predators across a range of thermal habitats, which requires elevated and relatively constant temperatures for efficient neurophysiological processing (the hypothesis underlying high cranial temperatures in billfish).

Future Directions

Although a significant amount of information exists on the physiological and biochemical adaptations of endothermic fishes, relatively little is known about how these processes are integrated in nature (88). Given the considerable advances in tagging technology, there is a tremendous potential to gain significant insight into

the physiology and ecology of these interesting and important apex oceanic predators. Combining tags with modern satellite remote-sensing techniques will enable us to put these magnificent animals in the context of their oceanic environment (61, 89).

REPRODUCTIVE PHYSIOLOGY

The limits on reproductive physiology have been a focus of physiological ecology since early field observations noted that animals in nature can exceed three to four times basal metabolic rate for extended periods of time during reproduction (97–101). Since these early observations, researchers have focused their analyses on the short-term evolutionary consequences of such physiological effort on fitness (102).

Reproduction is thought to be costly largely because of the energetic demands imposed on parents during the acquisition of resources for progeny (77, 99, 102, 103). Two fitness consequences have been the focus: the effects of energy expenditure on progeny survival (102) and the effects of energy expenditure on adult survival to future reproductive episodes. The former issue relates to the first fundamental trade-off of life history analysis (104), referred to as the offspring size and offspring number trade-off, whereas the latter issue relates to the second trade-off, referred to as costs of reproduction in parents (105). With one possible exception (106), the relationships between energy expenditure in the wild [expressed as daily energy expenditure (DEE) or field metabolic rate (FMR)] has not been simultaneously assessed for both components of fitness, even though such information might be useful in interpreting the phase of life history (progeny versus adult fitness component) that is most sensitive to energy limitation imposed on adults. In such situations, it is possible for the unmeasured component of fitness to be related to DEE (DEE of parent affects progeny survival), while the measured component of fitness is not correlated with DEE (DEE of parent does not affect adult survival). This would result in a failure to find an association between DEE and fitness, even though such an association exists.

In brief, researchers simultaneously assess field metabolic rate with the doubly labeled water (DLW) method (107, 108) to measure DEE on reproduction of lizards, birds, and mammals (109, 110). Estimates of DEE are often made in conjunction with detailed estimates of behavioral time-budgets (77, 103, 111, 112), which when used in conjunction with laboratory estimates (e.g., O₂ consumption) of each behavior (e.g., cost-of-flight, cost-of-hovering flight, running, lactation, etc.) can be used to partition DEE to specific metabolic episodes by integrating the behavior over time. Furthermore, direct comparisons of time-budget-derived DEE and DLW-derived DEE over the entire period during which DLW is measured also can test the validity of the DLW method.

As an important experimental adjunct to methods for assessing DEE, many researchers invariably manipulate reproductive effort by litter size or brood size; such manipulations (augmentation or reduction) (99, 111, 113–116) provide a

causal measure of the relationship between DEE and fitness. In addition, other researchers have used food deprivation experiments (to progeny) to increase effort expended by the parents (111, 117). This allows for the inference of direct causal effect of offspring number on parental DEE, and for the direct causal inference of the effect of offspring number (or physiological effort) on parental survival to future reproductive episodes, offspring survival, or the success of parents in producing offspring on future reproductive episodes. Other studies have compared differences in the DEE and energy investment between closely related species with different foraging behaviors (103), in different habitats (118), or between marine mammals and seabirds utilizing similar resources in the same habitat (119).

Analyses of the two life history trade-offs from a physiological perspective has had mixed results regarding the importance of physiological ceilings during reproduction as having a selective impact with cascading effects on fitness traits. Lack of a relation as a state of the real patterns must be conditioned upon the caveat noted above regarding the action of selection during adult versus progeny phases of the life history and its correlation with DEE in adults. In spite of this caveat, the discrepancies between the studies highlight the different physiological pathways in vertebrates for basic life history function [avian feeding strategies, huddling behavior on parental effort, granivory-insectivory (116, 120, 121) versus carnivory (111) or versus mammalian lactation (114, 119, 122)]. For example, in the European kestrel, *Falco tinnunculus*, manipulation of parental effort via clutch size manipulation has a clear effect on the elevation of parental effort in both parents, and the physiological effort has a clear impact on the survival of adult birds to a second clutch and future reproductive episodes (123, 124). Furthermore, food removal experiments indicate that kestrels are capable of nearly doubling energetic effort on a short-term basis (1.5 weeks) (111). Similar studies on a granivorous-insectivorous species, the great tit, *Parus major*, failed to find an associated link between DEE and fitness of cost of reproduction, even though manipulations of parental effort have demonstrated such links (125).

Similarly, in mammalian systems, detailed estimates of DEE for females during reproduction are available for the North American species the Golden-Mantled Ground Squirrel, *Spermophilus saturatus*, and red squirrels, *Tamiasciurus hudsonicus* (77, 114, 122). The most costly period of DEE for female squirrels is lactation. No correlation between litter size and DEE was found, but rather all females approached a similar physiological ceiling (114, 122). As patterns of reproductive costs and investment vary with body size, it would be useful to know how the patterns of investment vary in large mammals.

Although the energetic costs of reproduction have been studied in ungulates, primates, and pinnipeds, no study has assessed the relationship between DEE and fitness. Such fitness relations would be useful in understanding the role of physiology in shaping the evolution of life history patterns. A common feature of these highly precocial animals is that they always give birth to a single large offspring (126). Measurements of DEE during lactation in pinnipeds show two markedly different reproductive costs. The cost of reproduction in true seals (Phocidae) is quite economical (1.5–3 times BMR), whereas it is quite high (4–6 times BMR) in

sea lions and fur seals (Otariidae) (126). This in part is the result of the differences in the way that females forage and provision their offspring. True seal females provision their pup primarily from stored energy reserves, often fasting during lactation, whereas sea lions and fur seals intermittently forage at sea returning to suckle the pup on shore (126).

Reproductive Endocrinology

The examples of reproductive physiology in nature illustrate how laboratory analysis of the homeostatic processes of endocrine regulation has led to a series of elegant analyses of such homeostasis in extreme environments. The advent of radioimmunoassay of reproductive hormones in free-ranging animals revolutionized our view of the endocrine system in action. In addition, the ability to insert hormone-filled implants into free-ranging animals has allowed for an analysis of causation that rivals laboratory studies, albeit in an uncontrolled field setting.

Our goal in this brief review is not to treat the endocrine axes in complete detail but rather to provide an overview of how such tools have been useful in unravelling the complexities of hormone interaction in nature. This example is useful in that endocrine homeostasis is well characterized, as are the cascading effects on target physiological traits and reproductive physiology [reviewed in (127–129)]. Endocrine homeostasis during reproduction arises from the action of protein hormones (gonadotropins) secreted by the hypothalamus and pituitary, which stimulates the gonads to produce the sex-specific steroid hormones. The up-regulation in the production of these steroid hormones in turn down-regulates the production of the gonadotropins (Figure 15). This two-part endocrine system is referred to as the hypothalamic-pituitary-gonadal (HPG) axis, and it represents a negative regulatory loop in that steroid hormones have a set point that is not exceeded owing to the negative regulation exerted by the steroids on the gonadotropins. Given that levels of steroid hormones achieve stable population-specific values and that these steroids control many physiological processes, we can view this as the elements of physiological homeostasis. The steroid hormones in turn up-regulate the transcription of specific genes related to physiology through accessory DNA-binding carrier proteins and response elements on the DNA [e.g., estrogen response elements (ERE)]. This regulation of behavioral, metabolic, and other physiological traits has been the focus of field endocrinology.

The link between individual and environmental extreme is regulated by another endocrine axis, the hypothalamic-pituitary-adrenal (HPA) axis (128, 129). Short-term and long-term regulations of sex steroids and their effects on metabolism are governed by both transient and chronic elevation of glucocorticosteroids, which have a regulatory function and a basic metabolic function. The glucocorticoids such as corticosterone can down-regulate production of the reproductive hormones (129) and also override the effects of steroid hormones on the expression of physiological and behavioral traits (128). In addition, corticosterone per se regulates gluconeogenesis and the breakdown of muscle tissue, serving as a direct regulator of metabolic physiology (130). It is for these reasons that field endocrinology

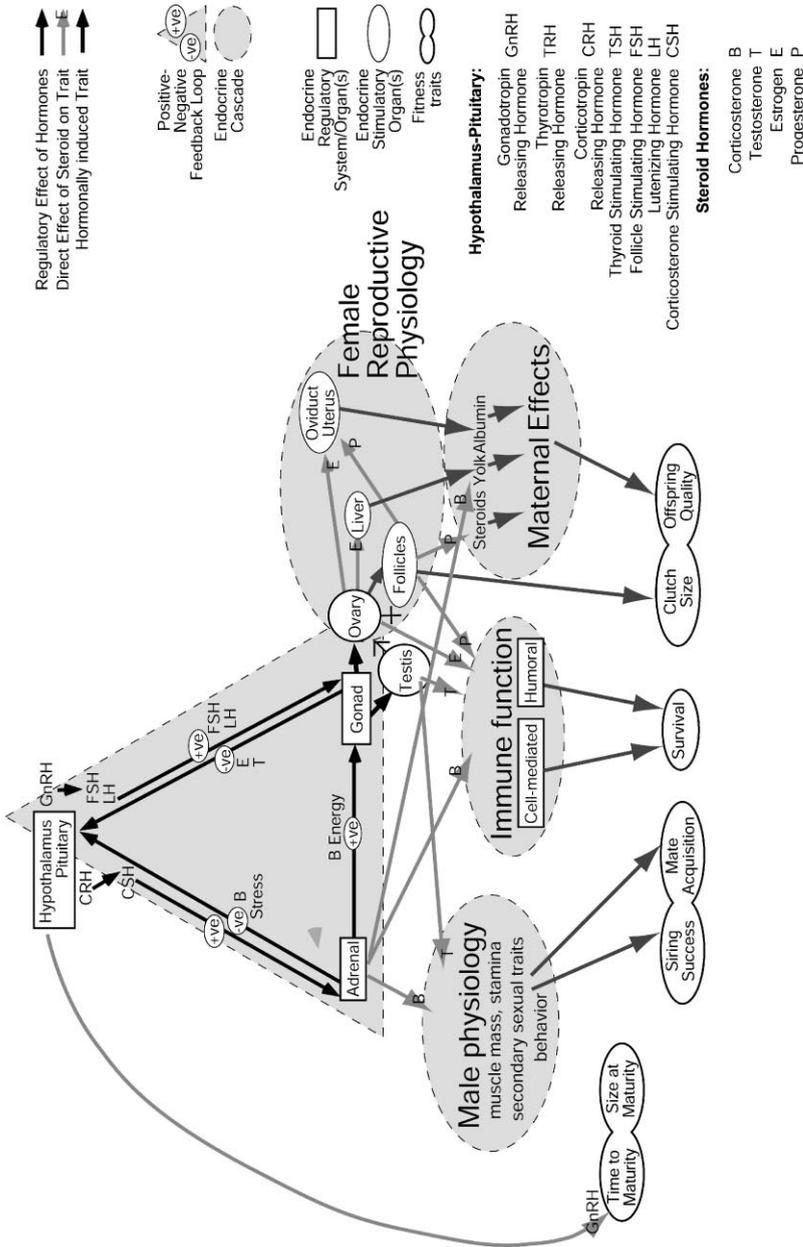


Figure 15 Endocrine homeostasis in endocrine system arises from the interaction of several endocrine axes. Endocrine homeostasis has cascading effects on a suite of physiological traits. The top triangle depicts the hypothalamic-pituitary-gonadal (HPG) axis and hypothalamic-pituitary-adrenal (HPA) axis. See text for a description of the hormone cascade. The endocrine system has control over loci that govern physiological and life history traits specific to male physiology and female reproductive physiology, which contribute to fitness (*bottom ovals*).

has focused on the action of corticosterone on a diverse array of physiological traits and how such traits are modulated when environmental conditions become either unfavorable or favorable for reproduction. In addition, corticosterone not only regulates physiology in the context of abiotic stressors (128), it also regulates physiology in the context of biotic stressors such as predators and conspecifics (129). Salient observations of nesting birds during stressful events such as snowstorms indicate that corticosterone plays a major role in modulating reproduction during stress, reducing levels of the gonadotropin lutenizing hormone (LH), which may be related to nest abandonment (131).

The actual control of reproductive physiology has turned out to be decidedly complicated (Figure 13). Initial experiments using hormone implants in nature typically involved a treatment in which a single hormone implant was tested against sham-implanted subjects (132). It was rapidly apparent that hormone interactions or hormone and environment interactions were largely responsible for the effects on physiology. Multihormone implants were developed or hormone implants were used in tandem with other manipulations ([e.g., food manipulation (133)] to further test these findings. Another basic technique was to manipulate a salient axis of the endocrine system and measure the corresponding changes in other axes [e.g., effect of gonadotropin-releasing hormone on LH and testosterone (134), effect of corticosterone of the HPA on LH of the HPG, effect of hypothalamus-pituitary control over corticosterone response (135)]. Another approach was to implant combinations of hormones to study the effect of hormone interaction on behavior and physiology (e.g., overriding effect of corticosterone over testosterone, corticosterone plus testosterone, no corticosterone, no testosterone sham-implants) (136). Manipulations of reproductive effort have also been used in tandem with measurement of plasma hormone changes (137).

The basic hypothesis concerning the role of corticosterone as a global signal of environmental stress has been invalidated by the observation that corticosterone has multiple avenues for modulating physiology. For example, the classic idea that corticosterone is immunosuppressive (129, 138) has been overturned with field implant experiments and immune challenge experiments (139). However, it is worth emphasizing that corticosterone has many effects on physiology in addition to affecting the immune system (128). Corticosterone enhances gluconeogenesis and thereby elevates blood glucose levels (128, 129), and such an effect may, at least in the short term, improve several aspects of condition including immunocompetence. Nevertheless, the role of corticosterone in modulating stressful environments has solid support from a number of studies (137, 140–142) and this information will be crucial in interpreting the action of corticosterone in stress during the expression of reproductive physiology.

Future Directions

Measurements of DEE during reproduction and its impacts on fitness are needed for other vertebrates including lizards, and more extensive assessment of fitness traits is required for mammals. While studies on lizards have focused on the

measurement of DEE (107, 109), none has yet applied the techniques of experimental manipulation that are currently available. In a similar vein, mammalian studies have relied on litter manipulations to test life history theory, but only recently have litter manipulations been applied in tandem with measurements of DEE (114). Furthermore, new methods of endocrine manipulations of litter size are available (e.g., follicle stimulating hormone), which have already been used in reptilian systems. Although there are studies on the costs of reproduction in females and the impact of brood size manipulations, there are surprisingly few studies of the impact of elevated male hormones on male DEE, despite this protocol being widely used in the area of field behavioral ecology. A careful causal dissection of the impact of male reproductive hormones and energy would be most informative.

Such endocrine manipulations of life history traits are preferable over simple litter size manipulations in that hormones can trigger a physiological cascade of events and thus are more likely to capture all of the salient physiologically based costs (143). Surprisingly, the actual metabolic costs of immune challenges have not been assessed with DLW methods. It would be most informative to test animals in the wild with novel antigens and measure the cost of such immune assaults. Furthermore, such manipulations of immune function when carried out with manipulations of reproductive hormones (139) might address the synergistic impacts of immune and reproductive function on DEE and the existence of physiological ceilings during reproduction.

CONCLUDING REMARKS

We have just touched the surface of the considerable number of physiological investigations carried out in the field. However, it is apparent even from this limited review that a vast array of tools and approaches are available to address fundamental questions of physiological homeostasis and how these processes have evolved. Given that field physiology has its origins in comparative physiology, it is important to recognize the pitfalls if phylogeny is not appropriately considered (12, 110).

Recent phylogenetic methods that provide corrections for statistical biases have been developed owing to a lack of independence associated with taxonomically related species (144a). The method of phylogenetically independent contrasts is one of the most widely used methods, and it creates contrasts (e.g., the difference) between the values of extant taxa and hypothetical ancestral states that are constructed with branch lengths in the phylogeny. It is really a linear transformation of the data that constructs a data set of independent data points, removing the effect of phylogeny. Notably, these phylogenetic methods have been applied to the scaling of FMR (110). A previously reported difference in the scaling of FMR between marsupials (e.g., 0.58) and eutherian mammals (0.81) (109) is not supported when the allometric regression is corrected using the method of phylogenetically independent contrast (0.71 versus 0.82). Use of modern phylogenetic methods are preferable because the estimates of slope are unbiased by the distribution of phylogenetic data, even though some groups may be under-represented.

Field physiology has an important role in the maintenance of biodiversity and conservation. As the pace of habitat destruction, over-harvesting, and climate change increases it will be critical to understand which organism can accommodate to these human-induced alterations in their habitat. The effects of climate change are myriad (144, 145). Whereas the general trend is toward a higher mean temperature, regional climate models indicate that the changes will be more complex (145). Some habitats will become wetter, others dryer, some will get warmer, some will get more precipitation, and others may change very little. In all cases, an understanding of the physiological capability of organisms to tolerate these changes can come only from field investigations of the organism in its habitat as its response is multifaceted (144). This review has shown that animals have the capacity to respond to varying levels of food intake and/or energy expenditure during reproduction. Although a simple relationship is expected between reproductive output and cost, animals can accommodate considerable variation in energy intake and expenditure while still successfully producing offspring. Similarly, these responses are mediated by a complex endocrine system that is just beginning to be understood in the context of the environment. We have shown that some diving behaviors are fundamentally more difficult and thus likely to put specific organisms in greater jeopardy. Finally, endothermic tunas, billfish, and sharks are currently over-fished at a rate that cannot be sustained (146). All the examples used here have potential importance to the conservation of biodiversity because it is critical to know which organisms have physiological plasticity that can accommodate environmental change. Field physiology can and should have a role in solving these complex environmental issues and can at least help to identify the organisms most in need of help.

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Figure 8 An Australian sea lion, *Neophoca cinerea*, mother and her pup are shown with data loggers attached. The most forward device is a satellite transmitter, the middle device is a time swim-speed and depth recorder, and the last item is a VHF radio.

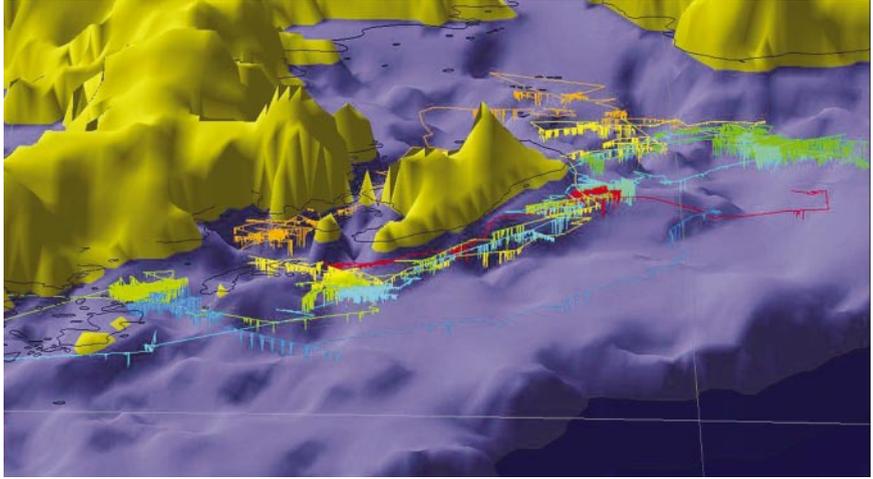


Figure 9 A pseudo three-dimensional representation of the diving behavior and movement patterns of crabeater seals, *Lobodon carcinophagus*, studied in the Western Antarctic Peninsula near Adelaide Island. Data were collected with a satellite-linked data relay. Image produced by the Sea Mammal Research Unit St. Andrews Scotland (D.P. Costa, J.M. Burns & M.A. Fedak, unpublished data).

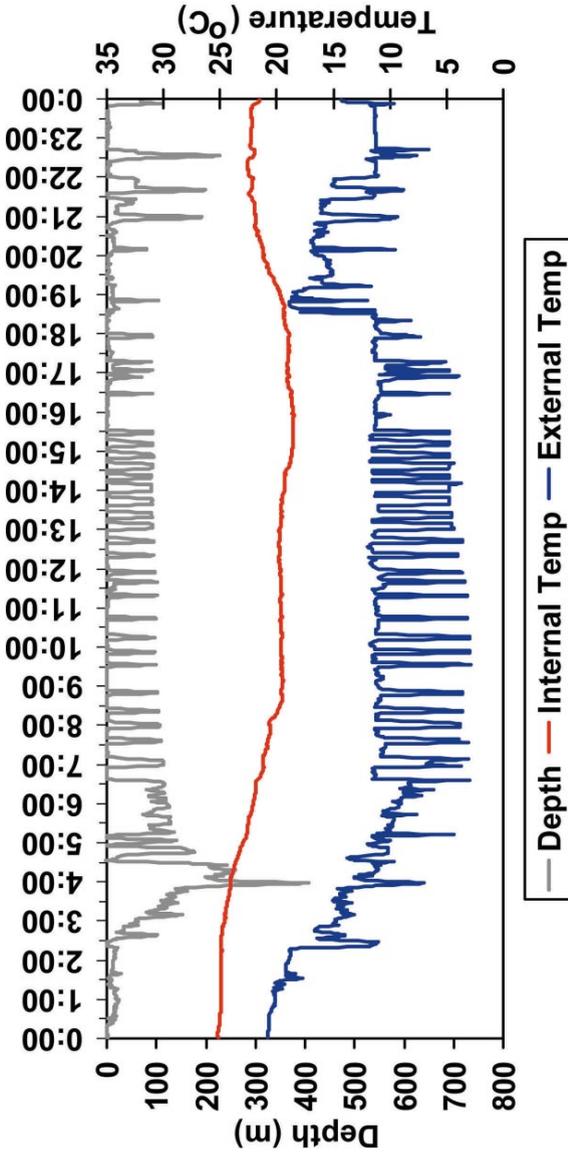


Figure 13 A 24-h record obtained with an archival data logger recovered from an Atlantic bluefin tuna. The gray line at the top of the graph shows the depth of the animal; the middle red line shows that the internal body temperature remains constant in spite of the dramatic variation in ambient water temperature. Data are unpublished and courtesy of B. Block, Stanford University.

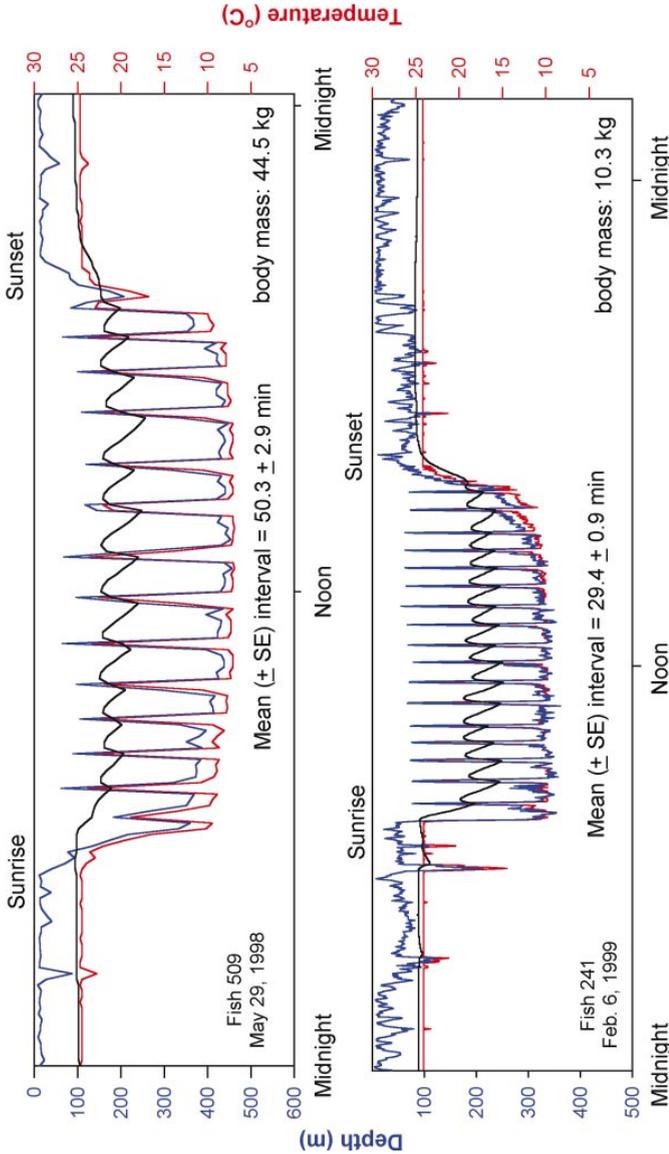


Figure 14 Two 24-h records derived from a large (44.5 kg) and small (10.3 kg) big-eye tuna, *Thunnus obesus*, off the main Hawaiian Islands, using archival data loggers. The blue line shows the animal's depth, the red line shows ambient water temperature, and the black line is the internal body temperature. Notice that due to its larger body size and greater thermal inertia, the larger fish can remain in the deeper colder water longer before it has to return to the surface to warm up (96).



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