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Physiological Ecology in the 21st Century: Advancements in Biologging Science[1]

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SYNOPSIS. Top pelagic predators such as tunas, sharks, marine turtles and mammals have historically been difficult to study due to their large body size and vast range over the oceanic habitat. In recent years the development of small microprocessor-based data storage tags that are surgically implanted or satellite-linked provide marine researchers a novel avenue for examining the movements, physiology and behaviors of pelagic animals in the wild. When biological and physical data obtained from the tags are combined with satellite derived sea surface temperature and ocean color data, the relationships between the movements, behaviors and physical ocean environment can be examined. Tag-bearing marine animals can function as autonomous ocean profilers providing oceanographic data wherever their long migrations take them. The biologging science is providing ecological physiologists with new insights into the seasonal movements, habitat utilization, breeding behaviors and population structures in of marine vertebrates. In addition, the data are revealing migration corridors, hot spots and physical oceanographic patterns that are key to understanding how organisms such as bluefin tunas use the open ocean environment. In the 21st century as ecosystem degradation and global warming continue to threaten the existence of species on Earth, the field of physiological ecology will play a more pivotal role in conservation biology.

INTRODUCTION

Examining animals in their natural environments has been a traditional pursuit of the animal physiologist. Throughout the history of our field, researchers have conducted physiological and behavioral studies of free-living animals using innovative techniques, novel engineering and natural ingenuity (Scholander, 1940; Schmidt-Nielsen, 1998; Kooyman, 1965, 2004; Carey and Lawson, 1973; Gunn and Block, 2001; Costa and Sinervo, 2004). Physiologists and ecologists have long been interested in knowing where animals go and how they function in response to natural environments. Today, as once distinct science fields merge even more, we ''physiological ecologists,'' share keen interests in studying the linkages between life history traits, physiology and environment (Bartholomew, 1986). By conducting careful measurements on free-ranging animals, physiological ecologists have revealed insights into how animals occupy diverse environments and the limitations of physiological performance. Our data enables us to consider how natural selection acts in the real world, beyond the confines of the laboratory. In the 21st century the field of physiological ecology will reemerge, and advance at an accelerated pace due to new technological advances (*e.g.*, biologging science) and multi-disciplinary approaches. This will enable collection of field data that will answer questions about how animals use their environment.

Knowledge of the physiology of free ranging animals at sea has been especially challenging to obtain. This is primarily due to the constraints of available technologies in the ocean environment. Attaching data storage tags as well as satellite transmitting devices to the backs of large marine animals that surface intermittently to breathe has proven to be a successful technique for gathering data (Fedak *et al.*, 2002; Kooyman, 2004; Costa and Sinervo, 2004). Pelagic animals have historically been the most difficult to study due to their large size, speed and range over vast oceanic habitats. The challenges of working with oceanic animals far at sea, on platforms that are rarely stable, has limited acquisition of data on their distribution, physiology and ecology. New approaches involving acoustics, satellite telemetry and archival tags are rapidly changing the capacity to conduct ecosystem-scale science in the open sea (Gunn and Block, 2001; Block *et al.*, 2003; Klimley *et al.*, 2003; Fedak, 2004; Costa and Sinervo, 2004; Kooyman, 2004).

We live in an age of new technology. Computers, microprocessors and global telecommunications networks provide the ability to locate animals more precisely on the planet with the Global Positioning System or Service Argos. Emerging electronic tagging technology, and rapid advances in ocean observation via remote sensing herald a new era for marine physiologists. Modern tags have powerful microprocessors, increased memory, and improved sensors thus providing more precise and rapid sampling of the environment. Remote sensing satellites provide global views at higher resolutions, more useful for integrating environmental data with animal collected data. Together these new tools are advancing the science of biologging and improving the capacity of the physiologist to tackle unanswered ecological questions.

The advances in electronic tags, data logging techniques, data acquisition and processing, and real-time data communications make the tracking of marine animals over distant waters practical. Previous techno-

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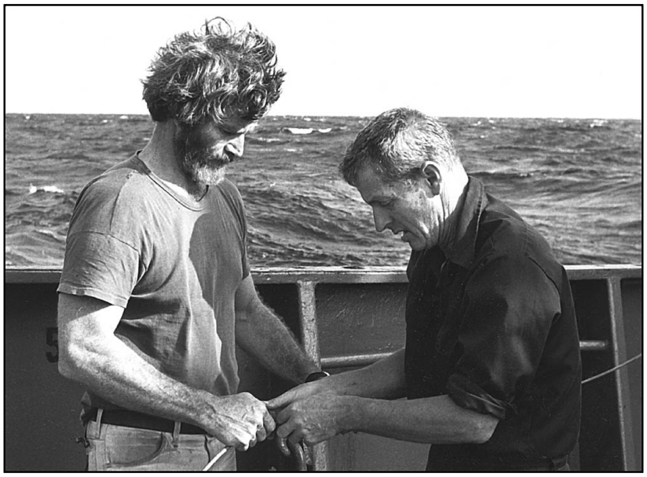

FIG. 1. Two pioneers of ecological physiology of highly migratory fish at sea for tagging swordfish. Francis G. Carey and John Kanwisher about 1977.

logical limitations for determining the location of animals that remain completely submerged, such as tunas, have recently been overcome using implantable archival tags and pop-off satellite tags that provide the end user with light intensity and sea surface temperature measurements that are used to estimate position (Block *et al.*, 2001*a*, *b*; Teo *et al.*, 2004). These new electronic tags have built upon the success of the earlier generations of devices (time depth recorders, TDRs) pioneered by Kooyman (1965, 2004) and colleagues (1976; Hill *et al.*, 1983), the acoustic multiplex tags of Carey, Kanwisher and their colleagues (Fig. 1, Carey *et al.*, 1973) and the new generations of fish archival tags (Metcalfe and Arnold, 1997; Itoh *et al.*, 2003*a*, *b*; Gunn and Block, 2001). Researchers studying seabirds have also been pivotal in the development of technology as their needs required miniaturization in parallel to requirements for fish. Bird researchers built smaller TDRS to study avian migrations, physiology and behavior (Ancel *et al.*, 1997; Kooyman *et al.*, 1996; Butler and Jones, 1997; Wilson *et al.*, 1998, 2002).

Currently, fish ‘‘archival tags’’ are miniature tags (0.5 to 20 grams), that record pressure, external and internal temperature, salinity and ambient light. They provide records of environmental variables and behavior of the animal carrying the tags and provide locations with good precision (Welch and Eveson, 1999; Teo *et al.*, 2004). The tags are most often surgically implanted inside the peritoneal cavity and in the case of tunas, a stalk protruding from the tag carries the irradiance and water temperature sensors. Internal temperature sensors are also carried within the body of the tag and record body temperature. Fish carry the tags for months or years before recovery in highly exploitable species (*e.g.*, salmon and tunas), creating the need for low power consumption when data logging. Tag manufacturers and users have been improving geolocation estimations using astronomical algorithms, threshold light geolocation methods and sea surface temperature (Wilson *et al.*, 1992; Hill, 1994; Hill and Braun, 2001; Ekstrom, 2004; Teo *et al.*, 2004) to the point where one can estimate the position of a fish that is completely submerged with 0.5 to 1.8° accuracy. Tracks as long as 3.5 to 4.5 years on animals that remain completely submerged have been recorded (Block *et al.*, 2001*a*, and unpublished data). This permits observing the ontogeny of movement patterns in relationship to body size and comparison of adolescent and mature behaviors.

In the past decade, these rapidly evolving techniques for biologging science and remote sensing are advancing how physiologists study top predators at sea. This is of critical importance given that the conservation of highly migratory vertebrates represents one (*e.g.*, leatherback sea turtles, bluefin tunas) of the major challenges of marine conservation. For example, surgical implantation in tunas of archival tags with sensors capable of delivering *in situ* data from freely swimming fish in the open ocean provide critical information on habitat use, thermal biology and movement paths important for stock structure analyses (Block *et al.*, 2001*a*; Boehlert *et al.*, 2001; Schaefer and Fuller, 2002). We can reconstruct the environment through which an animal swims, the speed, acceleration and in some cases the gait of the moving animals. We can examine their diving behaviors, cardiac and thermal physiology, swimming speed and biomechanics (Williams, 2000; Weimerskirch *et al.*, 1997; Costa and Sinervo, 2004). This enables researchers to better understand the physiological limitations that are critical to the performance of animals in a natural world, in turn providing a more complete understanding of environmental preferences and limitations, energetics, species range and potentially fitness. The length of the tag records provides an ontogenetic view of physiological performance. In the case of bluefin, the techniques provide rapid information on the ecological niche expansion into sub-polar waters with increasing body size.

The new biologging tags have led to the rapid expansion in the physiological literature of studies recording physiology and behavior of animals in natural habitats (Costa and Sinervo, 2004; Kooyman, 2004; Fedak, 2004; Gunn and Block, 2001; Arnold and Dewar, 2001). Does this do any more than tell us new stories about how individual species live in the natural world? Importantly, we can now define how animals from common clades such as *Thunnus*, the Lamnid sharks, or the rorquals discretely use their oceanic niches, allowing comparison of physiological capacities, species tolerances, niche separation, and performance within dynamic, natural environments. In many cases, the results are critical for understanding population structure and are essential for management decisions involving over-exploited species. Understanding the ontogeny of habitat use, or the changes of geographic assemblages in association with climate variability is of key importance to understanding the future of dynamic boom-or-bust marine fish communities.

The successful deployment of a new generation of satellite tagging technology, archival tags, and novel acoustic listening stations is rapidly advancing the study of oceanic vertebrates and large squid (Metcalfe and Arnold, 1997; Block *et al.*, 1998*a*, *b*, 2001*a*, *b*; Lutcavage *et al.*, 1999; Klimley and Holloway, 1999; Klimley, *et al.*, 2003; Kitagawa, 2001, 2002*a*, *b*, *c*; McConnell *et al.*, 1992; Costa, 1993; Bost *et al.*, 1997; Kirwood and Robertson, 1997; Gunn *et al.*, 1999; Costa and Sinervo, 2004). These new techniques are providing major advances necessary to understand the distributions of oceanic organisms in relationship to their dynamic environment. As more environmental information is gathered from archival-tagged animals, new insights about their individual behaviors, physiology and performance are generated. This enables researchers to study how animals respond to environmental variability on daily, seasonal, and inter-annual time scales. This research comes at a vital time as increasing concerns about monitoring animal movements in relationship to climate change and overexploitation become key to preserving remaining biodiversity and better understanding our planet. We have increasingly noticed that oceanic realms are not inexhaustible. The need for rapid acquisition of knowledge for drafting plans for marine protected areas, has the physiological ecologists spearheading numerous innovative electronic tagging studies to discern how animals use their oceanic environment.

Fish and microchips

The precise measurements now being made on free swimming marine fish and sharks are made possible by recent advances in electronic tag design and satellite telemetry. Previously, fish physiologists were limited in the telemetry realm by their need to follow individual animals using acoustic technologies (Arnold and Dewar, 2001; Gunn and Block, 2001). The design concept for ultrasonic acoustic tags has changed little since the work conducted by Yuen (1970) and Carey and Lawson (1973); ultrasonic frequencies are generated by driving an annular ceramic transducer at its resonant frequency, and the frequency of the signal transmitted is determined by the transducer's diameter. Up until the mid 1990s, acoustic studies primarily focused on collecting data from a single animal (a fish) equipped with the ultrasonic tag at a given time. The tag encodes the data as a series of ultrasonic pulses transmitted through the water column from a hydrophone and are decoded by a receiver on a ship. The expense was often high, due to the costs of the ship, the personnel and the electronic tags. Acoustic tag technology progressed significantly through the last decade but the fundamental limitations remained the same. As electronic circuitry controlling tag function has been miniaturized with surface mounting of components and integrated circuit technology, tags have become smaller. However, the constraints of transducer size and battery volume remain when large range or extended transmission life is required. Acoustic tags now incorporate sensors that allow measurements of speed, cardiac physiology and behaviour. When the tags are used in combination with real-time measurements of the physical and biological environment, acoustic tags become a powerful tool in examining environmental preferences of tuna (Block *et al.*, 1997; Brill *et al.*, 1999; Dagorn *et al.*, 2000).

Few studies on tunas prior to the use of the new archival tags, have been designed to acquire data from more than one fish or sensor at a time. To record two types of data from a single fish simultaneously requires using two tags of different frequencies (Marcinek *et al.*, 2001*b*) or a multiplex acoustic tag (Block *et al.*, 1992). A major advancement in acoustic tagging has been in the use of listening stations. Klimley and Holloway, (1999); Klimley *et al.* (2003), Welch and colleagues (2003) have pioneered using acoustic tags that download data to electronic monitors fixed in position. The receivers record electronic ''zip codes'' from transmitting tags as the fish swims by. By attaching the receiver to floating buoy systems, researchers have recorded the residency of tunas at seamounts and fish aggregating devices, and salmon smolts leaving natal streams. Klimley *et al.*, (2003) revealed a synchronicity in visits to open ocean seamounts that provides information on how these fish use the buoys as feeding centers. Advances will soon lead to using these listening stations for fish as pelagic receivers where physiological data sets can be archived and downloaded as the fish swim by. Newer innovations such as pop-up receivers and acoustically linked modems for data retrieval will rapidly advance this type of acoustic telemetry.

Archival tags represent a significant change from acoustic techniques and permit an increasing level of sophistication for sampling design. The advancement in sensor technology, permitting more precise pressure and temperature measurements increases the accuracy of the collected data. Although data logging (TDR) tags have been used extensively on marine mammals, birds and reptiles for three decades (Kooyman, 2004) a major emphasis on building smaller tags with increased memory capacity, and lower cost came from the tuna and salmon communities in the 1980s and 1990s (Gunn and Block, 2001). The need for small tags for marine birds such as penguins, paralleled the requirements for fish and has led to multiple engineering teams solving similar problems, including construction of smaller tags that have reduced drag costs. In the fish community, the specific requirement that the ''TDRs'' be built with external sensor stalks for sampling the light intensity and ambient temperature, has been a severe hurdle that manufacturers have had to overcome. At least three manufacturers (Northwest Marine Technologies, Wildlife Computers and Lotek, Inc) have responded to the requirements for externally carried sensors for tags surgically implanted in the peritoneal cavity. The dependence on recovery of data from the recapture of the archival tagged fish in exploited fisheries has resulted in a large need to deploy large numbers of tags, motivating a reduction in cost per tag deployment. The three companies in the new market, created a slightly competitive atmosphere that sped-up progress, and also helped to reduce prices of archival tags to all users of the technology. Effective power management routines, and smaller batteries are critical to increasing the duration and frequency of data recording while decreasing the size of the packages and the physiological cost of carrying the electronic tags. These new generations of tags and a growing number of post-processing algorithms, are now permitting the recording and display of the most detailed information to date, on the behavior, physiology and environmental preferences of the animals carrying the tags. The longest records of animals in the wild are being logged by northern bluefin tuna in the Atlantic and Pacific oceans. Records approaching 5 years of movements, internal body temperature data, depth and oceanography are recorded on a 25 gram tag. The major drawback of the techniques are the limitation of use in fisheries with high exploitation rates. The rapid advances in this tag technique have led to a wealth of new information on the physiology, behavior and distribution of northern and southern bluefin, bigeye, yellowfin and skipjack tunas (Block *et al.*, 1998*b*; Block *et al.*, 2001*a*, *b*; Block *et al.*, 2003; Schaefer and Fuller, 2002; Kitagawa, 2000, 2001, 2002*a*, *b*, *c*, 2003).

Satellite-linked data recorders have expanded our understanding of the fine-scale movements of a number of marine animals (Priede, 1984; McConnell *et al.*, 1992; Prince *et al.*, 1992; Renaud and Carpenter 1994; Pauley and Christensen, 1995; Kooyman *et al.*, 1996; Ancel, *et al.*, 1997; Bost *et al.*, 1997; Block *et al.*, 1998*b*; Polovina *et al.*, 2000; Weimerskirch and Wilson, 2000; Weimerskirch *et al.*, 2000; Shaffer *et al.*, 2003; Weng and Block, 2004). Since the antenna on the satellite transmitter must be out of the water to communicate with the satellite, the technology has mainly been used on air-breathing vertebrates, which surface regularly. Data on each animal's behavior and environment are collected by the tag, summarized, and transmitted back via the Argos satellite system. The Argos system consists of modules attached to the NOAA low-orbiting weather satellites. These modules record the transmissions from satellite tags and later download these data back to Earth. Service ARGOS (Toulouse, France or Landover, MD) then processes these data. Currently, tags are set up to make multiple transmissions to increase the chance that an orbiting satellite receives at least three signals during a pass. Satellite pass durations vary between 3 and 20 minutes. Repetition rates cannot exceed once every 45 seconds, without special permission. ARGOS can also provide the location of the tag based on these transmissions. Locations are based primarily on 3 levels of accuracy and range from 150 to 1,000 meters (Vincent *et al.*, 2002). As these are polar orbiting satellites the coverage is greatest at high latitudes and poorest at the equator. Increasing efforts to merge GPS archival tags and ARGOS technologies may permit rapid improvement in the accuracy of positioning an animal in the coming decade.

For large fish or squid that remain continuously submerged, the ability to transmit to the Argos satellites is not possible. For these organisms, pop-up satellite archival tags were recently developed (Block *et al.*, 1998; Lutcavage *et al.*, 1999; Block *et al.*, 2001*a*, *b*; Marcinek *et al.*, 2001*b*). Pop-up satellite tags combine data storage tags with satellite transmitters. These tags are secured to the animal where they collect data in a similar fashion to the archival fish tags described above. At a predetermined time the tag releases from the animal, floats to the surface and downloads the collected data to the Argos satellites, which calculate a final location. The tag's final position is calculated using the Doppler shift of the transmitted radio frequency in successive uplinks received during one pass to the Argos system of satellites. Importantly, the pop-up satellite tags are fisheries independent; they do not require retrieval for data acquisition. The key innovation in the pop-up satellite archival tag is the development of smaller platform terminal transmitters (PTTs) that are small enough for external attachment on fish, sharks, sea turtles and a wide variety of mammals. Two companies, Microwave Telemetry and Wildlife Computers in collaboration with Seimac, Inc., produced the first generations of these tags.

The first pop-up satellite tags functioned as single point tags and provided an end-point radio transmitted location and a small archive of ambient temperature data (Block *et al.*, 1998*a*; Lutcavage *et al.*, 1999). Second generation pop-up satellite tags record light intensity, pressure and ambient temperature allowing estimation of position to be calculated with proprietary software from the manufacturer (Hill and Braun, 2001; Teo *et al.*, 2004). These tags provide data on daily geolocation for each animal based on light and sea surface temperature measurements, depth and ambient temperature as well as physical oceanographic data. Information stored on the tag is only transmitted after the user-specified time for detachment and surfacing. Pop-up satellite tags have been deployed on a wide variety of fish including Atlantic and Pacific bluefin tuna, yellowfin, albacore, halibut, mola, mantas, blue, black and striped marlin, tarpon and at least a dozen species of sharks (Gunn and Block, 2001; Boustany *et al.*, 2002; Graves *et al.*, 2001; Weng and Block, 2004).

Several new innovations for satellite tags originate from applications initially built for the fish research community. The development of a small ''bobcat'' PTT by Seimac, Inc. that was then incorporated into the design of the pop-up satellite tags provided the opportunity for Roger Hill of Wildlife Computers, Inc. to build new and smaller satellite tags (single position only tags, SPOT) applicable to a wider array of marine animals (Block *et al.*, 2003). The major pioneer in the fish telemetry realm, Frank Carey, conducted his last experiments by placing satellite tags on blue sharks.

His design in collaboration with the Sea Mammal Research Unit, was large in size, but worked extremely well. Carey proved that blue sharks came to the surface to bask regularly, and showed the research community that we could reliably track sharks using this behavioral thermoregulatory strategy for uplinking radio transmissions linking gill breathing animals to Earth orbiting satellites. The single position only tag (SPOT) currently being used on sharks is similar to the traditional satellite tag used by Carey; however, it has as an advantage, a small size (40 × 20 × 12 mm) and weight (25 g) that make it feasible for attachment to the dorsal fin of sharks, the head of a seal and the backs of sea turtles. Currently Block, Holts, Weng and colleagues have deployed this type of direct uplinking satellite tag on four species of sharks. The tags are providing the capacity for daily uplinks. Some species such as salmon sharks, *Lamna ditropis*, have been followed for over two years (Weng and Block, unpublished data). Increasing the capacity to record and archive physiological variables (body temperature, cardiac physiology) and then uplink-stored data to satellites will emerge by 2005. This opens the door for long-term thermal physiology studies on sharks. The Sea Mammal Research Unit also makes Satellite Relayed Data Loggers with advanced algorithms for data compression (Fedak *et al.*, 2001) that permit uplink of data on ambient temperature, speed and depth preferences. These tags are extraordinarily successful at storing data on dive patterns and oceanography, but due to large size are currently restricted to large mammals and sea turtles (Fedak, 2004).

The new electronic tag designs provide the necessary tools to address fundamental questions in biological oceanography concerning the distribution, behavior, and critical habitats of pelagic fish as well as marine birds, reptiles and mammals (Guinet *et al.*, 1997; Polovina *et al.*, 2000; Weimerskirch *et al.*, 1997, 2002; Costa *et al.*, 2001; Boustany *et al.*, 2002; Costa and Gales, 2003). Integration of the diverse data sets about physiology, ocean basin scale movements, and oceanography—results in a new type of bioinformatics. The data management and the development of new algorithms for data analysis remains the most challenging aspect of this new era. We will be able to answer questions such as: How do animals move through the physical structure of the environment to migrate or to locate food concentrations? How do they respond to the varying physical environment? How does habitat selection take place? Where are the migration corridors, and why? What temperatures the animals prefer and continuous recordings of body temperature will become commonplace. How do populations and species respond to climate variability, and decadal oscillations in productivity?

Physiologists in the 21st century will continue to make rapid advances and have increasing opportunities to study animals in their real world environs. This in turn will provide a suite of 'firsts' concerning information on the energetics of feeding and breeding migrations (Fig. 2), the costs of locomotion, the foraging dynamics of prey capture, specific dynamic action, or cold induced bradycardia of sharks, fish and rays, and a more compete understanding of endothermic traits in tunas. New software for data analysis and display are developing rapidly and enabling physiological ecologists to capture how animals use the ocean environment and integrate this information with the animal-collected physiology and behavioral data. ''Near real time'' physiology is apparent in data features such as when and where feeding events occur in relationship to subsurface thermocline and chlorophyll fronts and the timing of diurnal thermal cycles. This permits physiologists the opportunity to study highly migratory pelagic animals in the largest biome of Earth and has enabled the integration of their biology with the oceanographic habitat, thus providing ecological insights.

Understanding animals in the pelagic ecosystem

Perhaps the greatest advance in bio-logging science will be the emergence of ecosystem physiology. A major challenge for the 21st century is discerning the impact of humans on the world's oceans and environment. It is becoming increasingly apparent that whether the issue is our appetite for fish, or our consumption of fossil fuels, we are having a major impact on Earth's environment and inhabitants. Our role as top predators and the changes we impart through our collective actions as we feed on the top of the food chain are not easy to measure. The context for our man-made experimentation is that we are changing a biosphere that we only barely understand. Because technological barriers have limited our ability to study the open sea, our ability has been limited to understand and mitigate human impacts. We have been limited in our ability to predict oceanographic patterns, or understand the relationships of organisms to their environment, via the coupling between habitat, production and survivorship of interactive organisms in the sea.

The pelagic ocean ecosystem is the largest and least understood biome on Earth. Open-ocean ecosystems are non-homogeneous and patterns in both physical and biological parameters are apparent. These patterns are influenced by large-scale oceanographic factors such as atmospheric coupling, oceanic currents, upwelling and large-scale climate variability such as seasonal, inter-annual or decadal changes (*e.g.*, Pacific decadal oscillation). As a result of the environmental variability, oceanic animals are not homogeneously distributed across the oceans, but aggregated in regions that meet their habitat requirements *(e.g.*, thermal tolerances) and associated needs for prey, reproduction and migration (Block *et al.*, 2003). The electronic tagging techniques will allow physiologists to identify ''hot spot'' regions permitting differentiation between preferred pelagic habitats between species.

Today's ocean ecosystems are under extreme stress, often changing at alarming rates, much of it driven by our ability with technological innovations, to fish al-

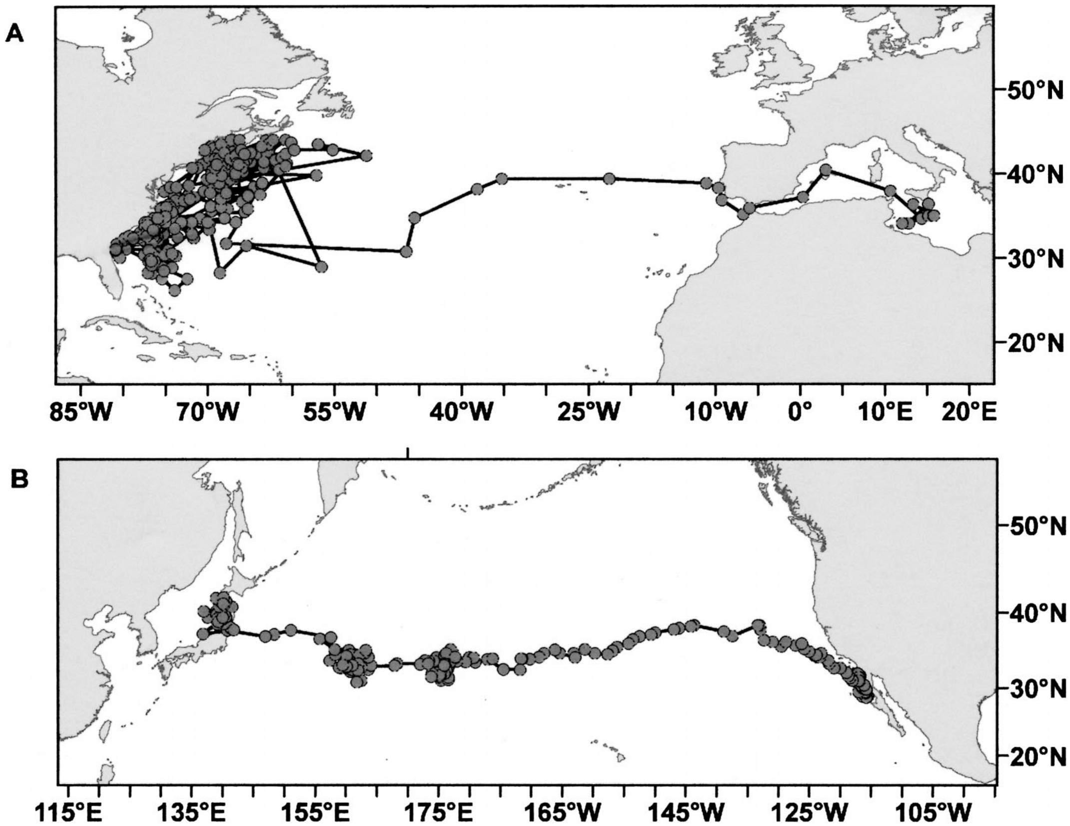

FIG. 2. (A) Archival tag track of a bluefin tuna followed over 3.8 years in the North Atlantic and Mediterranean Sea. The bluefin is tagged off North Carolina as an adolescent and returns to the Mediterranean presumably to spawn (From Block *et al.*, 2001*a*). (B) Track of a juvenile Pacific bluefin tuna released off Baja in 2002 and recovered in Japan in 2003. This 35 kg fish traveled over 6,000 nm in 9 months. Each point is an estimated position based on light-based longitude and sea surface temperature based latitude. Unpublished data of B. A. Block.

most anywhere in the ocean, and our poor understanding about the over-all consequences of our activities. The relentless pursuit of tunas and other large pelagic fishes by fisherman of many nations is causing the decline of not only these highly fecund populations of fish but of numerous species caught as bycatch (Myers and Worm, 2003). It is vital to the survival of the temperate tunas, sea turtles, sharks and some species of albatross (Hyrenback *et al.*, 2002) that we better understand the importance of marine habitats where these animals forage. Understanding how multiple animals use the ocean ecosystem simultaneously remains one of the more important questions for ''ecosystem'' based fisheries management.

The future conservation of ocean resources depends on understanding the naturally occurring variation in ocean ecosystems and the response of marine vertebrates on seasonal and multi-decadal time scales. The ability to link animal-derived data with oceanographic information has been vital to understanding the environment through which animals move. Much of the ocean is poorly known and researchers are learning that the animals themselves can collect oceanographic data vital for describing the environment around them (Campagana *et al.*, 2000; Boehlert *et al.*, 2001; Charassin *et al.*, 2002; Wilson *et al.*, 2002). When physiological, behavior, and location data acquired by electronic tags are merged with information on the physical and biological oceanography a wealth of new information is rapidly acquired.

Conservation physiology

Across the globe organismal physiologists have recognized the need for rapid advances in ''conservation physiology.'' I consider this area of physiology to entail the design of experiments studying live animals in natural conditions to further our knowledge for resource management and species conservation (*e.g.*, Block *et al.*, 2001a; Boustany *et al.*, 2002; see also Sharp and Dizon, 1978). As a field, we need to approach the challenges of managing living resources by better understanding the natural variation of environments and the suite of animal responses. Discerning the distinctions between climatic changes and human induced affects on exploited fisheries is challenging. Bio-logging science permits examination of animals in the context of the ocean environment and, in turn, provides a powerful tool for the conservation of biodiversity. Below are provided several case studies.

Our lack of understanding of the organizational principles and aggregating forces in the open sea ecosystems stems largely from limitations of available technology. Marine vertebrates including tunas, seabirds, sharks, sea turtles, pinnipeds and cetaceans use a pelagic ecosystem we barely understand. We would like to understand how pelagic predators use a highly dynamic and ephemeral habitat. Specifically, where are the aggregating places and why, and how do oceanic animals know where predictable regions of high productivity are? In a terrestrial context this scenario might be likened to gazelles, wildebeests, and lions gathering around a watering hole. In the marine realm, an example of a ''pelagic watering hole'' could be found in Monterey Bay on an October afternoon, where bluefin tuna, albacore, mola mola, leatherback sea turtles and blue whales might all be located within 30 km of one another. These fall periods are characterized by weakening of the wind stress that drives coastal upwelling, warm seasonal averages in ocean temperatures, and a nutrient rich water column with high seasonal averages of chlorophyll. Why and where additional regions of high biological activity occur farther from human eyes on ocean basin scales remains unstudied. We suspect that, like the watering holes of the African plains, these invisible, oceanic ''hotspots'' serve a critical role in the survival of pelagic organisms. We do not really understand how animals find these regions or what particular sensory physiology allows detection of the areas of high biological activity. Many of these regions will be predictable on annual or seasonal scales and depend upon features such as enhanced local production due to topographical features (*e.g.*, shelf breaks, seamounts) or regions of increased turbulence and mixing. These hot spots are likely regions that will be designated conservation corridors, and marine protected areas.

Conservation biology in terrestrial ecosystems has focused on identifying concentrations of vulnerable species in ''hot spot'' regions. Although it is generally accepted that these biodiversity hotspots occur and are important, surprisingly little is known about where such congregating spots for marine organisms in the open ocean occur and how they are maintained (Block *et al.*, 2003; Worm *et al.*, 2003). At the present time, there is little knowledge about how sea going animals orient toward major oceanographic features, how persistent such features are on seasonal or annual scales, or how major climatic events shape the patterns of movement and physiology of open ocean predators. How, for instance, the warming of the eastern Pacific in an El Nino Southern Oscillation event may limit cardiovascular and swimming performance of sardines and then precipitate higher trophic level affects, is completely unknown. How and why, in a cold Pacific decadal oscillation phase, increased upwelling production might favor a cold-temperate bluefin species over a tropical yellowfin tuna along one coast, while the opposite phenomenon would be observed on the opposite side of the Pacific basin (Chavez *et al.*, 2003). The underlying physiological and behavioral responses of ocean species to these dynamic processes are as yet an unrealized area of applied physiology.

NICHE EXPANSION AND INTERNATIONAL FISHERIES

Few animals on Earth engender passions and tensions like Atlantic bluefin tuna. Although Atlantic bluefin have been fished as far back as 7000 years BC (Desse and Desse-Berset, 1994; Maggio, 2000), and studied and revered by fishers as well as scientists, for most of recorded history, we know very little about the biology of this species. This dearth of knowledge is even more surprising when we consider the fact that a single fish can sell for $150,000 in the Tokyo fish market. Today over four million metric tons of tunas per year are landed globally. Most of the tuna catch consists of the more fecund tropical species such as skipjack, *Katsuwonnus pelamis*, and yellowfin tuna, *Thunnus albacares*. However, worldwide landings of the more temperate bluefin tuna group exceed all historical catches prior to our generation. While bluefin tunas are the most valuable, and among the most sought after tuna in the sea, physiologists have yet to measure their metabolic rate, accurately determine their growth curves, or recognize definite limits on when and where they breed. There is little time to discover the answers as the Southern bluefin tuna and the populations of the Northern Atlantic bluefin tuna have been considered in the past two decades for endangered species listings.

Northern bluefin tuna. The genus *Thunnus* of the family Scombridae includes not only the bluefin tunas (Atlantic bluefin tuna–*Thunnus thynnus*, Pacific bluefin tuna–*T. orientalis* and southern bluefin tuna–*T. maccoyii*), but in addition, many of the ocean's valuable fish, (yellowfin tuna–*T. albacares*, and big eye tunas–*T. obesus*). The bluefin tunas were first recognized as two independent species (Northern and Southern bluefin) based on subtle differences in morphological characters (Collette *et al.*, 2001). Northern bluefin tunas are recognized as morphologically, geographically and genetically separate species located in the Atlantic and Pacific oceans. The strongest argument for subdivision into Atlantic, Southern, and Pacific bluefins is based on ecology, with the distribution of three morphologically distinct bluefins into geographically separate oceans and spawning grounds.

All bluefins share similar life history traits that include large adult body sizes in comparison to other tunas and a high capacity for heat conservation via *retia mirabilia* in the circulation supporting the muscle, viscera and cranium (Carey and Teal, 1969; Carey and Lawson, 1973; Carey *et al.*, 1984). These traits enable mature bluefin tuna to maintain high body temperature (Fig. 3, Block *et al.*, 2001*a*). Biochemical and physiological studies on Atlantic bluefin demonstrate the presence of unique physiological features including large ventricular mass, high myoglobin concentrations, and high mitochondrial enzyme levels in cardiac and slow-twitch muscles (Marcinek *et al.*, 2001*a*, *b*). Bluefin tunas also possess hemoglobin that binds oxygen with high affinity in warm temperatures. Studies on bluefin tuna ventricles have found key biochemical ad-

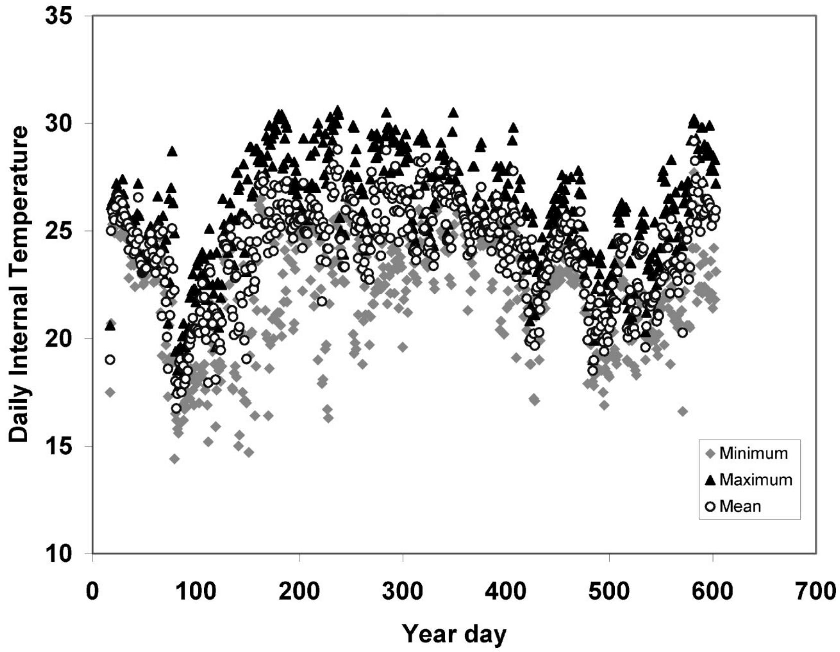

FIG. 3. Archival tagging of bluefin tuna reveals 600 days of body temperature of an 8 year old bluefin tuna. Maximum body temperatures occur after events of presumed feeding where specific dynamic action results in increased warming. Mean and maximum body temperatures provide high temperatures for the year that help to detect when a bluefin tuna is breeding (day 475). Unpublished data of B. A. Block and S. L. H. Teo.

aptations in the sarcoplasmic reticulum enzymes associated with calcium uptake that may underlie increased performance in cold waters and niche expansion (Landiera-Fernandez *et al.*, 2004, Fig. 4).

In order to examine questions pertaining to the physiology, ecology and behavior of tunas in their natural environment, extensive tagging projects were initiated, particularly as improved technology emerged. Northern and Southern Bluefin tunas were the first tunas to be electronically tagged with archival tags leading to a rapid increase in understanding of their remarkable physiology (Gunn and Block, 2001; Kitagawa *et al.*, 2001, 2002*a*, *b*, *c*, 2003). In the past decade, over 1,500 electronic tags have been placed on the three species of bluefin tuna in the Atlantic, Pacific and Southern oceans (Block *et al.*, 1998*a*, *b*, 2001*a*, *b*, 2003; Lutcavage *et al.*, 1999; Kitagawa *et al.*, 2000, 2002*a*, *b*, *c*, 2003; Gunn and Block, 2001). Tagging of sister taxa such as the bigeye and yellowfin tunas have resulted in similar success (Musyl *et al.*, 2001; Schaefer and Fuller, 2002).

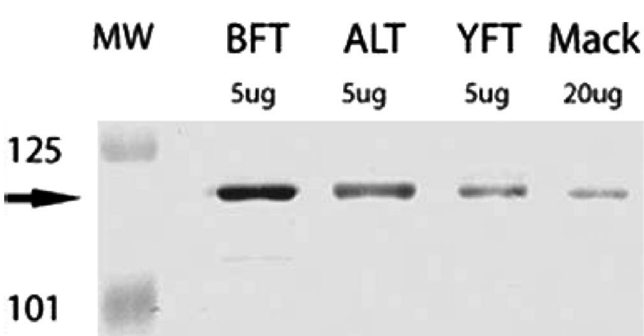

FIG. 4. Western Blot analysis of microsomes from different scombrid fish ventricles. MW, molecular weight markers (kDa); BFT, Pacific bluefin tuna; ALT, albacore tuna; YFT, yellowfin tuna; Mack, Pacific mackerel. The numbers above each lane indicate the micrograms of protein used. The arrow indicates the SERCA pump with an estimated M.W. of 110 kDa, calculated based on the relative mobility of the protein (Landiera-Fernandez *et al.*, 2004).

In the Atlantic, the Tag-A-Giant program of Stanford University and the Monterey Bay Aquarium was initiated in 1996 to examine seasonal movements, habitat utilization and environmental preferences in Atlantic bluefin tuna. To date, over 900 tags have been deployed on adolescent and mature bluefin tuna in the north Atlantic. The majority of these tagged bluefin were released off the coast of North Carolina where 600 bluefin tuna have been tagged with surgically implanted archival tags and 300 have been tagged with pop-up satellite tags. Additional satellite tag deployments have occurred in New England, the Gulf of Mexico and in the eastern Atlantic and Mediterranean Sea. Over 27% of the first generation of archival tags has been recovered and records spanning 4.5 years duration have been obtained (Fig. 1). This data set has provided over 13,000 daily position estimates of 7–12 year old Atlantic bluefin tuna, providing information on seasonal movements and preferred environments of these maturing late juvenile and adult ages, leading to a better understanding of their population structure.

Atlantic bluefin tuna are currently managed as two stocks in the Atlantic Ocean and Mediterranean Sea (National Research Council, 1994). It is hypothesized that the West Atlantic stock spawns in the warm waters of the Gulf of Mexico and the Straits of Florida and the East Atlantic stock in the Mediterranean Sea (National Research Council, 1994). Abundance of the West Atlantic stock of mature Atlantic bluefin tuna has decreased markedly since the 1970s in spite of the recovery plan that was put in place by the International Commission for the Conservation of Atlantic Tunas (ICCAT) in the early 1980's. The current management plan assumes that mixing between the two stocks occurs at a low rate (*i.e.,* 2%). However, recent archival and conventional tagging data indicate that fish in the West Atlantic cross to the East Atlantic at a rate that ranges from 10–30% (Block *et al.*, 2001*a*). Increased understanding of the migration patterns and level of mixing between the two stocks is crucial to improving the management and conservation of Atlantic bluefin tuna (National Research Council, 1994).

The data sets are providing the first true look at how bluefin use the open ocean environment (Fig. 2) and the of endothermy in bluefin in the wild (Fig. 3). The combined data sets from archival and pop-up satellite tags have shown a linkage between fish tagged in the West Atlantic and all the major fishery regions in the Atlantic Ocean and Mediterranean Sea (Block *et al.*, 2001*a*). We have strong indications of ontogenetic differences in bluefin migration patterns with adolescent fish showing residency to the western Atlantic shelf regions and restricted in latitude while mature fish are more pelagic, and capable of penetrating higher latitudes. The fidelity to the shelf locations (Carolina and the Gulf of Maine, Cape Cod) is associated with regions of high primary productivity and most likely represents bluefin feeding aggregations. The increased diffusion of older fish means that fish in these age groups have higher mixing rates across the Atlantic than do younger fish. The larger, and potentially mature fish have been tracked to known spawning grounds in the Gulf of Mexico and Mediterranean Sea as well as feeding grounds in the area east of the Flemish Cap. In addition to visitations to known spawning grounds, additional breeding areas may have been identified in the Caribbean Sea, Bahamas, Straits of Florida and offshore of North Carolina (Block *et al.*, 2001*a*). In addition, the data from the electronic tagging efforts are providing insights into seasonal movements, trans-Atlantic migrations, mixing rates, depth preferences, thermoregulatory biology and breeding behaviors. These data are critical for addressing the major management and conservation issues surrounding bluefin tuna in the Atlantic.

Of importance to the future management of the species is the need to identify the critical regions of overlap between western and eastern bluefin tuna populations, recording the fidelity to breeding grounds, and discerning the environmental preferences of bluefin on feeding and breeding grounds. We have reported that western-tagged Atlantic bluefin tuna are mixing on their feeding grounds but potentially sorting to distinct spawning grounds in the Gulf of Mexico and the eastern Mediterranean. We have demonstrated that as bluefin get larger their niche expands into more northern regions, exposing the animals to multiple international fisheries. Most recently, we have shown that bluefin of eastern origin are swimming in western seas. Thus, the tags are recording that bluefin's muscles, power-enhanced by the warmth of metabolic heat conservation and the radiating heat from digestion- are allowing this species access to patchily distributed food resources across entire ocean basins into surface water as cool as 9–10°C.

The electronic tag data has the potential to allow us to examine the relationships between feeding behavior, ocean productivity, and spawning locations as well as the environmental characteristics of the breeding grounds. Outcomes of the TAG program are critical for appropriate management by ICCAT and are providing the knowledge necessary for assessing population structure, mixing and movements in the North Atlantic. Similarly, the Pacific bluefin tuna tagging in the eastern Pacific as a part of the Tagging of Pacific Pelagics (TOPP) program will result in knowledge that will aid the future management and conservation of these economically and ecologically valuable resources on the west coast.

The Pacific bluefin (*Thunnus orientalis*) has a home range that spans the entire north Pacific, and young pre-adults apparently extend into the southeastern Pacific into Chilean waters. Based on larval surveys and the presence of juveniles there appears to be only one spawning region, occurring in the western Pacific (Sea of Japan, Philippine Sea). Until recently, the information that is available on northern bluefin tuna in eastern Pacific waters originates from conventional tagging studies or fisheries catch data (Bayliff *et al.*, 1991). A hypothesis emerged indicating that either late in the first year or early in the second year, some juvenile bluefin (55 cm fork length) make the 8,700 km journey to the western coast of North America (Bayliff *et al.*, 1991). Polovina (1996) hypothesized that the number of juveniles that made the trip east was dependent on the abundance of the Japanese sardine, which in turn was linked to the PDO. To learn more about the behaviors, migrations, thermal biology and habitat preferences of juvenile bluefin tuna, the Japanese initiated an archival tagging program in 1994 (Itoh *et al.*, 2003*a*; Kitagawa *et al.*, 2002*a*, *b*, *c*). Archival tags were implanted in the peritoneal cavity of 180 bluefin from 1994–1997. Of those a total of 70 tags have been recovered, 5 of which were recaptured near Japan, which appears to be an important nursery ground for Pacific bluefin in the western Pacific. Four of the tags recovered in the eastern Pacific documented the journey across the Pacific Ocean (Fig. 2B), providing more information on movements along the coast of California and Mexico.

To date our laboratory has deployed 200 archival tags in the eastern Pacific on bluefin tuna. Ninety of these archival tags have been recaptured, providing over 20,000 days of thermal biology, geolocation and vertical movements. The data provide information on the movements of Pacific bluefin off the California and Mexican coasts, showing significant penetration into cool high latitude waters by 30–40 kg Pacific bluefin tuna. During such phases the body temperature of the Pacific bluefin tuna cycles daily with means of 22–25°C in the daytime when surface waters as cool as 11–14°C are encountered. The tagging data are providing new insights into the seasonal movements, diel thermal body temperature cycles, feeding energetics and habitat utilization of Pacific bluefin tuna.

Pacific bluefin occur from the Baja peninsula to the waters offshore of Washington and Oregon. They take advantage of the high seasonal productivity in regions of the eastern Pacific with intense upwelling. In recent years, increasing numbers of Pacific bluefin tuna have appeared along the upwelling region of the eastern Pacific, suggestive of a trend of increased productivity associated with the PDO (Chavez *et al.*, 2003). The southern California bight region, Baja peninsula and waters offshore of central California are emerging as major regions of bluefin tuna residency. Four tunas tagged as a part of TOPP made substantial east to west migrations. One 15 kg fish migrated from the eastern Pacific to the offshore waters of Japan, back to North America before returning to Japan waters where it was recaptured. This migration covered over 18,000 nm in two years at liberty. These new archival data indicate the amazing migratory abilities of these endothermic fish, even when relatively small.

Of great interest is that as upwelling intensifies and production increases, the temperatures trend toward cooler norms. Pacific bluefin have molecular level specializations that allow them to function in these cool, prey rich waters (Blank *et al.*, 2002). Combining the tracking data and the molecular physiology suggests that climate shifts, and regional food-fish production changes (Sharp and Csirke, 1984; Sharp, 2003) due to atmosphere and ocean coupling are expressed as species shifts that occur in part, due to subtle difference in thermal specialization at the molecular level (Blank *et al.*, 2004; Landiera-Fernandez *et al.*, 2004). We have shown that cardiac and myocyte specialization of the Pacific bluefin tuna improved cardiac function in cooler waters relative to other tuna species. By combining the thermal habitat studies from archival tags with the physiological studies in the laboratory, it is possible to examine the linkage between the patterns of horizontal movement, vertical movement and seasonal variability with physiological specialization at the molecular level.

In both oceans, electronic tag data are revealing migration corridors, hot spots and behaviors in relation to physical oceanographic patterns that are key to understanding how northern bluefin tunas use the open ocean environment. The major results emerging are: 1) that the North American continental shelf is essential habitat for the early life history stages of both Atlantic and Pacific bluefin tuna, 2) the northern bluefin are capable of enormous migratory capacity as juveniles and adults, and 3) large bluefin have the ability to penetrate into the most northern latitudes where cooler water temperatures prevail. The new technologies provide data that are vital for obtaining insights on how these fish use their oceanic habitat and are required for new approaches to fisheries management and conservation. The common objective of both programs is to develop comprehensive models based on electronic tag data for discerning the essential fish habitat for bluefin tuna and predicting abundance and distribution based on meso-scale oceanographic features.

On the brink of extinction: the pacific leatherback

Electronic tagging is also being used by physiological ecologists to discern how Pacific and Atlantic Leatherback sea turtles use the ocean environment. Over the past 20 years leatherback turtles (*Dermochelys coriacea*) and other large marine sea turtles have experienced dramatic declines in their populations. The decline has been well established by physiologists focusing on the leatherback population at Parque Marino Las Baulas on the Guanacaste Coast of Costa Rica (Spotila *et al.*, 2000; Reina *et al.*, 2002; Ferraoli *et al.*, 2004; Hays *et al.*, 2004). Leatherback sea turtles in the eastern Pacific have been listed as critically endangered by the Convention on International Trade on Endangered Species (CITES) as breeding populations have declined by over 90% since 1988. Nesting data collected by Spotila *et al.* (2000) at Playa Grande, Costa Rica show a drop in females from over 1,350 turtles in 1988 to less than 100 individuals for 2001–2002. In addition to poaching on the nesting beaches, it appears that interactions with fisheries are contributing to the decline.

The reduction of nesting females occurred simultaneously with an increase in the swordfish longline fisheries in the Eastern Tropical Pacific. Satellite tracking studies of Costa Rica leatherback migrations, as well as studies with other Pacific leatherback colonies in Mexico, suggest that pelagic fisheries are incidentally catching females migrating to and from the nesting beaches and that this interaction is contributing to the recent population decline (Morreale *et al.*, 1996; Eckert and Sarti, 1997). Leatherbacks nesting in Costa Rica are thought to migrate along a bathymetric ridge that results in a biological corridor that traverse the Cocos Dome to Cocos Island. This corridor extends from Guanacaste, Costa Rica out to the Galapagos Islands and then out past Easter Island (Morreale *et al.*, 1996). The well-documented fisheries along this narrow migratory corridor produce a fisheries gauntlet through which these turtles must swim as they migrate to and from the beach every 2–5 years to nest and reproduce (Spotila *et al.*, 2000; Reina *et al.*, 2002).

The new satellite tagging technologies provide the first opportunity to protect turtles at sea. They will permit the collection of more detailed behavioral and environmental data, which can be uplinked daily, while simultaneously providing movement in the vertical habitat. This in turn provides real-time data of sea turtle movements linked to remote sensing data and to vertical water column data. There is an urgent need to learn where these ancient reptiles go while at sea, and to pinpoint regions of interactions with humans. By combining information on how the sea turtles use the ocean with data sets on where tuna and swordfish fishers have the greatest by catch per unit effort, we should be able to discern the interaction of leatherback sea turtles with human fishers and initiate protection measures. Using this information fisheries scientists and physiological ecologists can forge new policies for protecting the leatherback along its migratory corridors as well as in waters adjacent to critical nesting areas. These policies also lead to the creation of adaptive management strategies; including networks of temporally and spatially organized pelagic marine protected areas. The development of these policies will be driven by the availability of new data emerging from biologging science and remote sensing information. The ultimate goal of these efforts should be to prevent the extinction and to insure the recovery of leatherback sea turtles, and similar species in the Pacific.

Integration of multi-species tagging studies

Most physiological ecology studies in the past have focused on studying a single species. In the case of mammals and birds, the studies were almost always conducted at the nesting or rookery areas and eventually these animals' movements were followed into the open seas. Few attempted to examine interactions beyond a handful of individuals, let alone more than one species. Marine mammal biologists have led much of the field throughout the 1970s and 1980s with pioneering studies of diving physiology of pinnipeds (Kooyman, 2004; Costa and Sinervo, 2004). In the 21st century efforts will become more multi-disciplinary, with researcher focusing simultaneously on all the top predators.

A top down ecosystem view has been brought together in the Tagging of Pacific Pelagics program (TOPP), a field project for the Census of Marine Life program. The Census of Marine Life is an international research program that has launched a decade-long initiative designed to: 1) Determine what lived in the oceans in the past; 2) Understand what lives in the ocean today; and 3) Predict what will live in the future ocean. The TOPP project (www.toppcensus.org) is pioneering the use of electronic tagging methods to elucidate the pelagic habitat used by large marine vertebrates and squid in the North Pacific ecosystem. The TOPP program is utilizing a ''top-down'' approach to understanding the oceans. It complements the long dominant science initiatives that take the ''bottom-up'' approach to investigation of the oceans by examining nutrient cycles and primary productivity. These two complimentary investigative areas cover the two extremes of the food web which are intimately related, by the intermediary food fish and invertebrates. Marine predators selected for tagging in the TOPP program span broad ecological and trophic niches. A main goal of the program is to identify and characterize regions of high biological activity (''hot spots''), define migratory corridors, and define regions of high biodiversity overlap in pelagic ecosystems. A major outcome of the TOPP program will be a significant advance in our understanding of the linkages in pelagic ecosystems at several trophic levels and an ability to model the movements of pelagic predators throughout the North Pacific. In the TOPP program, a diverse set of species encompassing several ecological trophic levels are being tagged (sea birds, cetaceans, tunas, sea turtles, pinnipeds) and efforts will focus on defining regions of individual and multi-species concentrations, migratory corridors and biological productivity.

The TOPP program has a number of diverse aspects that will not only advance our knowledge but also the field of biologging. TOPP is discovering how to collect, utilize, and disseminate animal collected oceanographic data. The tagged animals can tell us where the areas of highest prey species abundances are, and help us understand more about why. The project will also produce new tools enabling researchers to observe and predict the movements of the animals in a dynamic ecological environment. Thus TOPP will lead to a deeper understanding of a number of apex predators and the key processes linking these oceanic species to their environment. As part of its mission, TOPP will be discovering new ways to collect, utilize and disseminate animal-collected oceanographic data. This knowledge will be used to model and predict the abundance and distribution of marine animals based on habitat preferences. TOPP research outcomes will provide a solid scientific foundation for management of pelagic ecosystems and lead to models predicting how fishing pressure and climate change will affect life in the oceans. Knowledge gained from this program will be critical for Pacific Ocean conservation and management.

Research on this large scale can only be accomplished with the development of a common set of computational and data management approaches and a philosophy for data dissemination in real time. TOPP is accomplishing this by promoting interdisciplinary science amongst physiologists, ecologists, oceanographers and computer scientists, a truly system science approach that has dwindled since the mid 1980s (*c.f.*, Fasham, 1984). Although multi-investigator research is common in physical sciences, it is a new endeavor in marine biology. TOPP will improve basic knowledge of oceans, species, and key processes linking apex predators to their ocean environs. These data can be used to predict and model the abundance and distributions of marine vertebrates based on habitat preferences. The knowledge gained from TOPP will be critical for Pacific Ocean resource management and vital for models that examine how fishing and global climate change affects life in the oceans. TOPP already provides an important new asset in global ocean observation.

IDENTIFYING HOT SPOTS IN OCEANIC ECOSYSTEMS

Compared to land animals very little is understood about the migration patterns of top predators in the oceans. A main goal of the program is to identify and characterize regions of high biological activity. Identifying pelagic hot spots on oceanic scales and linking these regions with oceanographic features is of high importance. New techniques for merging remote sensing data from satellites with data from tagged whales, sea birds, pinnipeds, fish, sharks and turtles are elucidating where these animals congregate along oceanic fronts. The integration of the movement data obtained with electronic tags and the physical and biological oceanography will enable scientists to predict the abundance and distribution of marine animals based on environmental forces shaping oceanic ecosystems. Discerning the key processes involved in ecosystem functioning and determining the impact of climate variability at various scales on the structure and function of open ocean pelagic ecosystems and their top predator species is vital to future protection.

Over the last two years TOPP has identified important temporal and spatial patterns in physical and biological features for Monterey Bay, the California Current, and the Southern California Bight. As the project expands, and grows to its full design capacity more features and relationships will be identified using both remotely-sensed data as well as the *in situ* environmental data that are obtained from the animal tags. By integrating animal tracks with oceanographic data, the regions of high biological activity will be characterized and models developed to predict their subsequent patterns of occurrence. The goal is to better identify the hot spot regions, to define how persistent the physical features are in space and time and to determine what role such places have in the life history of diverse taxa. The ultimate objective is the development of an understanding of the physical forcing, zooplankton production, prey abundance and distribution and apex predator behaviors to better elucidate oceanic ecosystem dynamics. We hypothesize that there exist in the ocean regions that can be delineated on the basis of biological and physical oceanographic characteristics outlined above. By identifying these regions, we can potentially prevent the degredation of top pelagic predators.

ANIMAL AS OCEAN SENSORS

Physiological ecologists have demonstrated that animals carrying oceanographic equipment can be of major importance to global efforts at ocean observation (Fedak, 2004). Animals with small tags are capable of sampling an environment that has historically been poorly studied, but is vital to development of better ocean models. Bluefin tuna, elephant seals and sharks offer unique platforms to carry instrumentation and to collect environmental information of high oceanographic value (Costa, 1993; Weimerskirch *et al.*, 1995; Le Boeuf *et al.*, 2000; Boehlert *et al.*, 2001; Charrassin *et al.*, 2002; Lyderson *et al.*, 2002; Fedak, 2004). As ocean animals such as tunas move on feeding and breeding migrations, they can provide direct *in situ* records of the temperature and depth profile, salinity, and light extinction in the water column. Such animal-borne ocean sensors not only report the animals' own environmental preferences, but also map ocean conditions in four dimensions (X, Y, Z and Time). This provides *in situ* records to calibrate satellite surface temperatures for example or measure ocean chlorophyll at depth. These animal "oceanographers" are very efficient at monitoring the physical characteristics of their changing environment.

Amongst the many species, the strong site fidelity, large size and survival makes elephant seals an idea animal for deployment of electronic tags as there is a 90% instrument recovery rate. From California rookeries, this species ranges widely over the northeastern Pacific on foraging trips that last from 2 to 9 months (Delong *et al.*, 1992). Migration patterns differ between the sexes; females migrate throughout the northeastern Pacific, while males migrate to destinations along the continental margin from coastal Oregon north to the Aleutian Islands. Males spend approximately four months at sea following the breeding season, returning to shore in summer to molt. After one month onshore, they return to sea for four months before returning to the rookery for the breeding season (Delong *et al.*, 1992; LeBoeuf, 1994; Stewart and De Long, 1995). Dives are routinely to 600 m, but can be as deep as 1,600 m (Delong and Stewart, 1991). With currently available tags, these animals have already proven to be capable of collecting large volumes of environmental temperature information throughout the central and eastern North Pacific. Northern elephant seals have also been used to develop and test a variety of environmental and physiological sensors including acoustic archival data loggers (Fletcher *et al.*, 1996; Burgess *et al.*, 1998) and heart rate recorders (Andrews *et al.*, 1997).

In the TOPP program the elephant seals are being used as a testing platform for new environmental sensors including a CTD tag. Deployments of seals with new instrumentation such as CTD tags have the potential to produce one of the largest data sets of *in situ* oceanography ever obtained on the North Pacific. We estimate that 100 seals deployed for 6 months will generate 1.2 million Temperature/Salinity depth profiles. While the entire Argo system will provide 100,000 T/S profiles per year from about 3,000 floats distributed over the global oceans. Considering the large amount of data that can be collected and the potential to dwarf any other data stream, it is paramount that a well-detailed quality control process is in place. TOPP and related programs are in the initial stages of expanding this technology set and applying the tools via many dozens of species, around the globe. The massive data set that will result for the existing ocean databases, more than justify the costs and effort this approach requires.

Training ecophysiologists for a multi-disciplinary future

In recent decades, there has been a marked decline in the numbers of graduate student and post doctoral researchers in the areas of integrated biology and physiological ecology. National funding agencies have focused on genomics. Fisheries agencies focus on improving mathematical stock assessments. There has been a corresponding decline in funding from national funding sources (*i.e.*, NSF) to address applied science, particularly in commercial fisheries and oceanic contexts. The knowledge needed to unravel the complexities of high seas populations, the response of predators to climate variation, the need for rigorous and large sampling and integration of the various data sets, exceeds the funds being made available from Federal funding agencies. The threat to marine species existence on Earth is very real. The Marine Mammal Protection Act has provided protection for large whales and seals, but marine fish and sea turtles will depend in part on the physiological ecologists of the 21st century to generate the critical habitat maps, ecological knowledge that will lead to new conservation policies and increased protection. We must act now with a growing sense of urgency and as a community to address these conservation issues in our lifetime.

Critical components of an international response will be the elevation of our field, physiological ecology, the sharing of our invigorated discipline with advanced biologging instrumentation, and the design of new sampling plans, data analysis and integration tools. Bioinformatics initiatives must encompass physiological ecology and these complex data sets as much as they have genomics. Overcoming the technical challenges above are equaled by the analytical challenges once the data are ashore. Integration of empirical data with modeling frameworks should prove to be of high value (Jonsen *et al.*, 2003). Understanding population structures and physiological ecology will be essential for building new concepts of how populations in marine ecosystems work. This implies movement toward strong international programs involving multiple partners. Too few funds are made available to create new information beyond tantalizing tidbits. Certainly we lack funding as a field to sustain the flow of new researchers through solid graduate training and into appropriate institutions where they could create the information needed to manage the remaining species. Increasing support for multi-disciplinary training programs that train students in observation, natural history, physiology, engineering and oceanography will assure that the technology that has granted humans the ability to harvest the sea's wealth can assure its protection for the next generation

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