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Part one
ENVIRONMENT, BIOLOGY AND FISHERIES
WHY FISHES OF THE OPEN OCEAN?

At last count, scientists had recognized more than 31,000 species of fish in the world, by far the largest order of vertebrate animals. However, of that number, only relatively few, perhaps several hundred species, might be thought of as fishes of the open ocean. Of course, this leads to the question of what exactly is the ‘open ocean’, and secondly, what defines the fishes that swim there.

Perhaps surprisingly, the open ocean has no widely accepted formal definition. In the context of this book, it is defined as the surface layer of the sea or ocean, to a depth of about 200 metres. The term ‘open ocean’ also conjures visions of the wide blue yonder, waters well away from land masses. In the context of this book, though, we will include in our definition of the open ocean waters over continental shelves, as well as waters around reef drop-offs, islands and atolls.

There have been a number of attempts to categorize marine fishes by habitat, all of which suffer from the same problem of fluid boundaries. Having said that, one system of classifying pelagic marine fishes, proposed by Russian ichthyologist Nikolai Parin, has considerable influence on the fishes selected for this book. Following Parin, I’ve grouped fishes into three categories according to the proportion of their lives spent in this open-ocean zone. This first group-

Permanent residents of the open ocean (‘holoepipelagic’ fishes)

Fish in this category include marlins, sailfish, tunas, dolphinfish, some flying fishes, sauries, some pomfrets, ocean sunfishes, the pelagic stingray, predatory pelagic sharks including the shortfin and longfin makos, the blue shark, silky and oceanic whitetip sharks and the surface filter-feeding sharks – the basking and whale sharks.

Below the habitat of these true surface dwellers live many midwater (mesopelagic) fishes, some of which make nightly excursions to surface waters and are therefore also included here. Many species in this category were hardly known at all before the advent of surface longlining – setting lines with hundreds or thousands of hooks suspended by buoys. This gear, set around the clock, not only catches the main target species (tuna, billfish, sharks) but also an assortment of these midwater
fishes. These include lancetfishes, oarfishes, opahs, the louvar, and some of the snake mackerels (family Gempylidae) such as the oilfish, escolar and the snake mackerel itself.

Other types of fishes in this category strongly associate with surface materials, such as drifting weed, debris, logs or even drifting invertebrates such as jellyfish. Examples include the tripletail, pelagic leatherjackets and oceanic puffers. And finally, the pilotfish, a small member of the jack family, spends its life swimming in close proximity to large pelagic fishes, especially oceanic whitetip, blue and whale sharks. The remoras have adopted a similar habit, but, rather than swim near large hosts, they attach themselves by means of highly modified dorsal fins and are therefore passively transported with their hosts to cover the same geographic ranges.

Dwellers of the open ocean for only part of their life cycles (‘meroepipelagic’ fishes)

Fishes in this category might spend only their adult lives in this zone, or at least part of their adult lives. Examples would include Atlantic and chinook salmon, which enter the surface layer of the open ocean only as early adults, having migrated from fresh water. They feed and mature in the pelagic zone for a number of years before returning to freshwater rivers to spawn. Other species in this category included here are the whale shark, which is mostly oceanic but gives birth in shallow waters, and some flying fishes, which must attach eggs to floating algae such as kelp. Another group of fishes in this category spend only their juvenile phase in the surface layer. A good example is the bluebottle fish, which spends its juvenile life in close association with the floating colonial siphonophore, the bluebottle or Portuguese man-of-war, but when mature, takes up a benthic (bottom) existence. Two other major groups
included here are some members of the jack family, Carangidae, and several of the Spanish mackerels (*Scomberomorus* spp.). Many jacks are found as juveniles around floating objects or buoys, while the juveniles of some, such as the golden trevally, mimic the pilotfish in looks and behavior, and in so doing, probably obtain similar protection and dispersal by swimming with their larger, highly mobile hosts.

**Occasional visitors to the open ocean (‘xenopeipelagic’ fishes)**

These are either coastal pelagic fishes which move offshore from time to time, or coastal species that associate with floating mats of weed or debris and drift into the open ocean as a result. Fishes in this category included here are some of the leatherjackets, chubs and some jacks, including, for example, the amberjack. Finally, also in this category are some species of fish which are normally coastal but which move offshore to take advantage of upwellings of nutrients or planktonic blooms, such as various herring and sardine species.

While these categories have helped guide the entries in this book, there remain some exceptions and outliers. A number of commercially or recreationally important species are largely coastal in their habitat preferences but may be encountered at the edge of the open-ocean habitat and are therefore included. In these cases, a general criterion for inclusion is that the species should be widespread, either occurring on both sides of ocean basins, or at least around offshore islands. Fishes in this category include the bluefish, bonefish, tarpon and roosterfish, a number of carangids (permit, queenfish, and some jacks/trevallies), most of the Spanish mackerels and several sharks and rays (bull shark, dusky shark and spotted eagle ray).

While relatively few fish species have adapted to life in the open ocean, those that have tend to be very successful. Many of the species included in this book have fully global distributions, occurring in all three major oceans as well as the Mediterranean Sea. The fishes of the open ocean depicted and described in these pages include the largest fishes on the planet – the whale shark, the basking shark and the manta ray. They also include the largest bony fishes in the world – the oceanic sunfish, the blue marlin, the black marlin and the Atlantic bluefin tuna. Some species, such as the streamlined wahoo and the sailfish, swim faster than any others, while several of the billfishes and tunas and sharks make regular transoceanic, or even interoceanic journeys. Some of these fishes, such as the skipjack tuna, are among the most prolific fish species on earth, supporting huge commercial fisheries that supply millions of people with affordable protein. The fishes of the open ocean are remarkable in many ways and it behoves us, as stewards of our marine resources, to manage and conserve them sustainably for the benefit and wonderment of all who will follow.
There is an apocryphal story of an angler fishing one pleasant morning with high hopes of a great day’s fishing. He hooks the first small baitfish of the day, but as he’s winding it in, a bonito takes it. As the excited angler attempts to land the unexpected bonus, a big yellowtail promptly grabs the bonito. The sudden screaming of the little bait reel loudens even more when a large yellowfin tuna engulfs the yellowtail in one swoop and heads for the horizon. The ensuing fight is long and hard, and then, just when the tuna is nearly within range of the gaff, a huge blue marlin appears from nowhere, swallows the tuna and so the fight is on again. With incredible skill, and by this time, well out to sea, the angler finally has the catch of a lifetime alongside the boat when suddenly … the little baitfish spits out the hook! Now, even if you don’t believe this fish tale, it does illustrate the simple concept of a linear food chain quite nicely. Old textbooks on biology often referred to these as food chains, in which each link connected different organisms in a direct line. But in reality, the way that organisms rely on each other for food is far more complex. Hence the term ‘food web’ was coined, quite aptly relaying the idea of an intricate interdependence of a whole suite of plants and animals within a vast, but relatively closed ecosystem. Here, we will explore the food web of the focus of this book – the food web of the upper layers of the open ocean.

**Ecosystems of pelagic fishes**

Pelagic fishes live in a somewhat unusual environment, often far from land, with little if any physical structure available. This habitat has been likened to a marine desert, since the availability of food is often very patchy, dependent on transport of nutrients from the land or in upwellings from the abyssal depths. Some areas may be rich in nutrients, and therefore are hotspots for marine life, while others may not contain much life at all. This world in which open-ocean fishes live is a complex self-contained ecosystem that maintains a rich and diverse fauna and flora on a vast scale. This environment extends from the ocean’s surface to perhaps 200 metres below – in reality a mere film on top of the world’s great oceans. But this thin and delicate layer contains the stuff of life – sunlight, oxygen and warmth.

The building blocks of all oceanic food webs are the phytoplankton – tiny single- or multi-celled floating plants which manufacture sugars by photosyn-
Tiny phytoplankton and zooplankton are key building blocks in the oceanic food web. Seapics.com/1q3-d/Peter Parks

A feeding frenzy of small tunas sends signals to other predators such as sharks, dolphins and seabirds. Julian Pepperell

A searching gannet hunts for surface-feeding tuna. Julian Pepperell
The food web of the open ocean is complex. This simplified illustration shows just some of the ways in which the whole ecosystem is interdependent on its component parts.
thesis. Nutrients are also necessary for plant growth, which in the open ocean are mainly derived from organic matter (dead animals and plants) formed by decomposition on the ocean floor and brought to the upper layers by upwelling currents. The abundant phytoplankton form the vast pastures which are grazed upon by the zooplankton—tiny animals including the larval forms of many invertebrates, especially crustaceans, and fishes. As well, the phytoplankton are the primary source of food for the teeming schools of filter-feeding anchovies, herrings and pilchards, not to mention probably the most abundant animal on earth, krill.

Oceanic food webs can be rather complicated. Small baitfishes such as anchovies, pilchards and sauries are the staple diet of a whole array of larger animals, including many species of predatory fish. These include tuna, sharks, dolphinfish, mackerel, wahoo, marlin, sailfish and swordfish.

From the time they are only a few centimetres long, all of these species hunt the seemingly defenceless baitfish schools. Other predators also take their turn to feast on this food supply. Dolphins and porpoises, which collectively number in their tens of millions, take their considerable share, as do many species of seabird, each specialized in the size and type of food they target. In fact, some species of seabird only eat small baitfish which are driven to the surface by feeding tuna. Without the assistance of tuna, the birds would have no source of food.

Squid also feast on anchovies and small fish, but they are also huge consumers of zooplankton, particularly the teeming masses of tiny crustaceans which form dense concentrations in the water column (clearly visible at night on any good depth sounder as this so-called scattering layer rises to the surface). And of course, the many species of oceanic squid themselves are a vital, often dominant component of the diets of many animals in different levels of the food web. Sperm whales, for example, eat squid almost exclusively, while broadbill swordfish are also particularly dependent on this abundant supply of protein.

Other components of this tangled web include marine turtles, which eat not only small fish, but also jellyfish and jellyfish-like plankton such as salps. Then there are the mighty baleen whales which filter great gulps of water through their
The largest animals of the open ocean are all filter feeders. Here, humpback whales lunge upwards through schools of anchovies, taking huge mouthfuls of water which they strain through their baleen plates.

seapics.com/
James Watt
baleen, or ‘whalebone’ plates. In the Arctic and Antarctic, these whales graze easily on krill, while in more temperate waters they take advantage of concentrations of baitfishes. Witness the annual appearance of dense schools of pilchards off the South African and Western Australian coasts which are always attended by pods of hungry minke whales.

On the subject of filter feeders, the largest fishes on the planet, the basking and whale sharks, also feed on the smallest organisms. Basking sharks do so by simply swimming through the plankton with mouth agape, while whale sharks more actively suck in mouthfuls of water containing small crustaceans and schooling fish, sometimes engulfing larger predators such as tuna in the process.

As mentioned, sharks are important components of the food web, consuming small fishes and squid in large quantities. But larger predatory sharks also prey on animals further up the web. As adults, some, such as the white shark, become specialized feeders on marine mammals, including seals, dolphins and even whales. The tiger shark has evolved the singular ability to bite through marine turtle shells – a particular favorite food item of this widespread shark. Even at the apex of one part of the food web, the large marlins and tunas are targeted food items for other predators, including large shortfin mako sharks and one particular species of toothed whale, the false killer whale. The latter appears to be a specialist predator of large oceanic fishes, having...
Jellyfishes and other coelenterates are a significant proportion of macroplanktonic biomass and are eaten by a surprising variety of fishes and other marine animals.

seapics.com/
Masa Ushioda
a very wide gape and relatively large teeth compared with other toothed whales.

Swimming the gauntlet

One fascinating aspect of the oceanic food web which makes it very different from land-based food webs is the general principle of larger fish eating smaller fish regardless of species. Many land animals, such as mammals and birds, produce large, well-developed young, and care for them until they are virtually adult-sized and have a good chance of survival. In the ocean, this is rarely the case. Most marine fish produce millions of eggs each year, which are simply released into the water, fertilized and left at the mercies of the currents. As each tiny larval fish grows towards adulthood, it must run a perilous gauntlet. Baby tuna and marlin can and will be eaten by any larger predatory fish, including larger tuna and marlin. It is not uncommon to find baby billfish inside the stomachs of species like dolphinfish, while small marlin bills can often be found embedded in the stomach lining of adult marlin. The danger of being small is probably why so many pelagic fishes have very rapid growth rates. ‘Grow or die’ could well be the motto of the mixed layer. It is indeed a fish-eat-fish world.

Those who fish can gain some idea of the food web immediately influencing their catch by conducting simple dietary studies on landed fish. Open the stomach of any pelagic fish and chances are you will find a fairly broad range of food items. The main food groups you might expect to see would be crustaceans, molluscs and, of course, fish. The crustaceans might include the larvae of crabs (a very common dietary item of tuna and, sometimes, marlin), free-swimming crabs, prawns, shrimps and, quite commonly, stomatopods – praying mantis-like creatures also known as prawn killers. Molluscs in the pelagic fish diet consist almost entirely of cephalopods; that is, squid, cuttlefish, octopuses (including paper nautilus and many species of pelagic octopus) and the occasional tiger nautilus. Often, the indigestible beaks of squid are all that remain of this very important group of prey. Most stomachs will contain fish, or at least the remains of fish, sometimes, one species of fish completely dominating the diet. I well remember the first sailfish I dissected, the stomach of which was completely crammed with small pelagic toadfish. On other occasions, several different species of fish of different sizes might be found. For example, large blue marlin in Hawaii are often found to contain very small boxfish and triggerfish in their stomachs. Since marlin do not possess comb-like gill rakers which other species use to sift small food items from the water column, it would appear that large marlin pick off these tiny fishes, one by one.

Breaking the web

Marine ecosystems were in existence for hundreds of millions of years before human predators began to take ever-increasing quantities of organisms from different levels of the food web. Looking at just some of the fisheries of the open ocean which have developed only in the past few decades, annual catches of several levels of food web animals have reached staggering levels. Global annual catches of skipjack tuna have recently topped two million tonnes, over half

One of millions. The developing egg of a dolphinfish, Coryphaena hippurus. Many open-ocean fishes produce huge numbers of eggs that float near the surface, where they are fed upon by other fishes and specialist seabirds. Syd Kraul, Pacific Planktonics
of which is taken in the western Pacific Ocean. More than one million tonnes of yellowfin tuna are also removed annually from the world’s oceans, a high proportion of the catch consisting of juvenile fish. Catches of sardines and squid would each also top the million tonne mark, while the take of smaller fishes such as anchovies would be well over 10 million tonnes.

The Peruvian anchovy holds the dubious distinction of being the most heavily exploited fish. The fishery for this tiny filter feeder, which was mainly converted into dried fishmeal, increased to a peak of over 13 million tonnes in 1971, but then almost completely collapsed and catches remained very low until the 1990s. The primary cause of the collapse is now thought to be a strong El Niño event, but many also maintain that intensive fishing must take at least some of the blame. Regardless of what or who caused the demise of these baitfish, it was clear that the animals which depended on the baitfish, such as seabirds and larger fishes, were affected when their primary food source diminished so dramatically.

The removal of such huge quantities of biomass from oceanic food webs raises two very big questions: Are such catches sustainable, and do they have any effect on the food webs themselves? For example, is there any discernible effect on prey species of removing large numbers of predatory fishes such as tuna and billfish, or conversely, does the removal of many thousands of tonnes of baitfish, squid or krill have any effect on predators higher up the web? Other secondary questions might include: Are these prey items, in terms of both species and size, being actively selected, or is the feeding of billfishes and other predators primarily (or entirely) opportunistic? Is prey (food) limiting at any stage of the life cycle of predatory fishes? Do populations of predatory fishes ‘boom or bust’ depending on prey availability? What is the total biomass of predatory fishes in a given area at a given time, and what biomass of prey is required to sustain the predator biomass?

Models of the oceanic ecosystem
Historically, fisheries science has tended to be based on single species. For example, studies on striped bass, summer flounder or skipjack tuna would concentrate on considerations of the life cycle of that particular species – its reproduction, age and growth rates, and mortality rates (from natural causes and from fishing) being the primary concerns. Dietary studies might be done also, but these would be secondary to the central study. Such
an approach would result in a reasonable understanding of the biology of a particular species, but in isolation from the rest of its ecosystem. Studies might even have included the effects of environmental variables on the organism, such as temperature or currents, but effects of or on other organisms were rarely considered in detail.

As our concept of ecosystems has improved, so too has the way in which animals within an ecosystem are studied. And with the great advances in computing power over the past several decades, sophisticated ‘models’ of entire ecosystems, and therefore food webs, can now be generated.

Such models can be used, at least in theory, to see what might happen if fish or other organisms are depleted at a given trophic level. However, a major problem with such computer models is that they rely completely on the quality of the information fed into them. So, while we have fairly good information on the biology and life cycles of some of the more commercially important species, such as skipjack and yellowfin tuna, little is known about critical parts of the food web, such as the biology of zooplankton, or of the many species of oceanic squid. As the saying goes, ‘garbage in, garbage out’, so with such major uncertainties about key elements, these models as they stand may be interesting, but they are still some way off from being used as predictive tools in fisheries management. What the models do show is that we need to know a lot more about the basic biology of many of the building blocks of food webs. In fact, so little is known about the biology of many of the building blocks of the oceanic food web that caution must be the primary concern in any development of any new fishery within this complex system.

Competing with other predators

One interesting argument has arisen from time to time to suggest that exploitation of fish and other organisms by humans is not necessarily a major problem. This stems from the idea that all of the animals which eat fish consume such huge quantities that the human part of the equation must be relatively minor. Such comparisons suggest that quantities consumed by seals, whales, dolphins and seabirds may even be one or more orders of magnitude greater than commercial (and recreational) catches.
While these arguments imply direct competition between humans and marine animals for the same resources, several important points need to be made. Commercial and recreational catches consist largely of finfish, while the diets of whales, dolphins and seabirds include high proportions of cephalopods (squid and octopus) and crustaceans. Seals certainly target fish, some of which are also caught by people, but they also eat a lot of squid. As well, many of the fishes being consumed by marine mammals and birds are not the same species as those targeted by humans, or if they are, they are not caught at the same sizes. Many of the most abundant species of seabirds, for example, eat very small fishes, or even fish eggs, while it is also known that whales rarely compete directly with humans for the same fish stocks.

So, even though these sorts of simple comparisons don’t tell us a lot about direct competition between humans, fishes and other marine animals, they do help to focus on the connections between human use and the oceanic food web. We know that predation at all levels within the food web has existed in the oceans for eons, and that such predation is the cause of a large component of what is called ‘natural mortality’ of fishes and other marine organisms. The very recent introduction of the human element into ancient food webs is a new and poorly understood additional pressure on these natural systems and it is therefore risky to increase exploitation on already existing large scales before we have a fuller understanding of the whole picture. We can coexist with and within these food webs. We just have to learn more, and take care at every step along the way.
Part two

GUIDE TO THE FISHES
5

Billfishes

BILLFISHES
The blue marlin is a true giant of the ocean. Its confirmed maximum size of 820 kg (1805 lb) makes it the second largest teleost (bony) fish, after the oceanic sunfish, Mola mola. Blue marlin occur in all three of the world’s major oceans. The Indo-Pacific populations have always been regarded as a single species, but blue marlin of the Atlantic and the Indo-Pacific have long been considered by some scientists to be separate species — Makaira nigricans in the Atlantic and Makaira mazara in the Indo-Pacific. The only feature described as different between the two is the pattern of the lateral line. On the surface, the lateral line of blue marlin is virtually invisible, but forms a ‘chicken-wire’ like pattern on the underside of the skin, the ‘mesh’ of which is smaller in Atlantic fish compared with those from the Indo-Pacific. However, more recent genetic studies indicate that these differences are insufficient to warrant their separation into separate species.

The blue marlin can be identified by its relatively high, pointed first dorsal fin (usually about two-thirds the maximum body depth), its folding pectoral fins and its proportionally large first anal fin. Other features are its relatively short lower jaw, and its gunmetal blue-gray color after death. A further feature to separate blue marlin from black marlin is that in the blue, the second dorsal fin is anterior to the second anal fin, whereas in the black marlin, the relative fin positions are the other way round.

The distribution of blue marlin is circumtropical, extending in summer to about 45° latitude in both hemispheres. Blue marlin are the most tropical of the istiophorid billfishes, as well as the most oceanic. They are normally found near islands or in the open ocean throughout their range, not usually being strongly associated with continental shelves (as is the black marlin).

The main recreational fishing areas for blue marlin around the world tend to be near islands. These include Hawaii in the Pacific, Mauritius in the Indian, the Caribbean islands in the Atlantic as well as many smaller islands in each ocean.
These islands are all tropical to subtropical, and appear to be locations of seasonal spawning for blue marlin.

Hawaii and Mauritius are well-known ‘hot spots’ for the occurrence of large, probably spawning female blue marlin, but in the Atlantic, relatively few very large – 454 kg (1000 lb) plus – specimens had been recorded until the 1990s. However, within several years of the discovery of large blue marlin around the island of Madeira, more thousand-pound blue marlin had been caught from those waters than had been taken during the long history of game fishing in the entire Atlantic Ocean. These fish were found to be not in spawning condition, and over time, their occurrence near Madeira has proven to be as enigmatic as it is unpredictable.

The majority of blue marlin have been tagged by recreational anglers in the Atlantic Ocean, mainly from the eastern United States and in the Caribbean. Over 30 years, tens of thousands of blue marlin have been tagged in the region, and hundreds recaptured. Movements of tagged fish have been extensive, with several transatlantic crossings being recorded. The most startling recapture, however, was a fish tagged off South Carolina and recaptured three years later near Mauritius in the Indian Ocean – the first proven movement between two oceans for any billfish (Atlantic to Indian).

In the Pacific, tagging of blue marlin off southwestern United States and Hawaii has revealed some very extensive movements as well. The most notable of these was a blue marlin tagged off Hawaii that was recaptured near Taiwan. Off Australia, even though over 5000 blue marlin have been tagged and released, there have only been 17 recaptures to date. Again, however, one of these was highly noteworthy. This was a blue marlin tagged off the Australian southeast coast, and recaptured 18 months later by a Japanese longliner 300 nautical miles south of Sri Lanka – the second interoceanic movement of a pelagic fish (Pacific to Indian) and again, a blue marlin.

The two largest billfish ever weighed and verified, both caught off Hawaii, were blue marlin. The largest weighed 820 kg (1805 lb) and was landed by a party of novice anglers aboard a charter boat off Honolulu in 1971. The second heaviest billfish weighed 753 kg (1656 lb) and was caught off Kona, Hawaii, in 1984. There are many anecdotal reports of blue marlin weighing in excess of 2000 lb (909 kg) – even as high as 2600 lb (1180 kg) – being caught by commercial longline ves-
sels, but it is not possible to verify any of these accounts.

There have been several studies of the growth rates of blue marlin, based on examination of their bony parts, in particular, fin spines and otoliths (ear bones). These studies have tended to assume that rings or other regular marks each represent one year of growth, but this has not been verified for blue marlin. One study which assumed annual growth rings estimated a 70 kg (154 lb) male blue marlin to be six years old; however, if blue marlin grow at a similar rate to black marlin (and they may not), then a fish of this size would only be about two to three years old.

By examining what are assumed to be daily growth rings on otoliths of very small fish, the early growth rate of blue marlin does appear to be very rapid, reaching 30 kg (66 lb) within the first year. It is theorized that all of the billfishes initially grow in length very quickly, presumably in order to be able to outswim predators as soon as possible. This is also an explanation for why very small billfish are rarely caught — it may simply be because they don’t stay small for very long.

According to early Japanese studies, blue marlin apparently have extensive spawning areas throughout the tropical and subtropical Pacific, Indian and Atlantic oceans. This picture is based almost entirely on the occurrence of larval blue marlin over very broad areas of these three oceans, and also assumes that billfish larvae have been correctly identified in these surveys.

Spawning adult blue marlin do appear to be patchily distributed, and are mainly found in seasonal aggregations around isolated islands. Around Hawaii, it has been found that nearly 80 per cent of the blue marlin landed during summer are males, mostly less than about 90 kg (200 lb) in size. Female fish caught at the same time cover a much greater size range, from as small as 22 kg (48 lb) to over 600 kg (1320 lb). Examination of the gonads of these fish has shown that spawning of blue marlin, at least at the latitude of Hawaii, is highly seasonal and predictable. Similar results have been obtained at Mauritius, indicating that
blue marlin are apparently able to locate remote islands as the spawning season approaches.

A 400 kg (880 lb) blue marlin may produce as many as 150 million eggs, each a little over 1 mm in diameter. As is the case for other billfishes, fertilization is external, and hatching of the tiny larvae occurs at the surface within two days. One recent study suggests that female blue marlin (as well as sailfish and white marlin) may spawn as many as four times in one season, but it is also speculated that spawning frequency may be much higher.

As blue marlin larvae grow, they differ from all other billfishes in that they do not develop a bill until they reach quite a large size – over 5 kg (11 lb) and 1 metre in length. This feature suggests that all of the other billfishes (broadbill excluded) form a relatively closely related group, with blue marlin representing an offshoot or outlier species.

The first attempts to track billfish after release, using a tag which emitted sonic pulses, were carried out on blue marlin off Hawaii in the early 1970s. Equipment failure and shark attack took their toll, but several successful tracks were obtained, paving the way for the more sophisticated technology of the next two decades. In the next study, six blue marlin, all caught by rod and reel, were tracked off Kona, Hawaii, for up to 48 hours. For the first few hours after release, vertical movements were somewhat erratic; however, fish then tended to settle into relatively predictable behavior patterns. Cruising speed averaged about two knots, and the great majority of time was spent within the so-called ‘mixed layer’ to a depth of about 80 metres, the level of the thermocline. Thus, vertical movements of the marlin oscillated between the surface and the thermocline, with occasional brief forays into colder, deeper water. This was the first proof of the highly surface-oriented behavior of any marlin species, and has proven to be very important in understanding catch rates by commercial longlining fleets using hooks which are set above and below the thermocline.

Perhaps the most interesting finding which emerged from this, and subsequent work using more sophisticated electronic tags, is that the depth at which blue marlin swim is strongly influenced by time of day. During daylight hours, fish tend to swim deeper, often near the thermocline, whereas at sunset, behavior changes and they become much more surface-oriented during the night. What is unknown at this stage is whether feeding still takes place at night. Use of popup satellite tags over much longer periods showed that vertical behavior remains relatively predictable. There is a tendency for fish to keep moving away from their release points, but parallel to the coast, throughout the tracking periods, one fish moving over 160 km away from its release point in four days.

Like most of the other Istiophoridae billfishes, the blue marlin is an incidental bycatch of the tuna longline fleets of the world. In addition, significant numbers are also taken as a bycatch of purse seine vessels which set their nets around floating logs. Stock assessment studies in the Atlantic Ocean strongly point to over-exploitation of blue marlin in that region, but in the Pacific, it appears that blue marlin stocks may be stable.
The black marlin is the least common of the world’s four species of marlin and, as a result, is one of the least studied and least understood of the billfishes. This is one of the largest of the teleost (bony) fishes in the world, growing to over 4 metres in length and up to 709 kg (1560 lb) in weight.

The main feature which sets the black marlin apart from all other billfishes is its rigid pectoral fins. In adults, these fins cannot be folded against the body, even with reasonable force. It should be noted, however, that very small fish have flexible pectoral fins, the calcification of the pectoral joint which causes this rigidity not occurring until a size of about 10 to 15 kg (20 to 30 lb). Another diagnostic feature is the position of the second dorsal and anal fins. The black marlin is the only istiophorid in which the second dorsal fin is anterior to the second anal fin – a feature which holds for all sizes. Lastly, the dorsal fin of the black marlin is the lowest of all of the istiophorids, measuring no more than half the maximum body depth in adults.

Although black marlin are distributed throughout the Indo-Pacific between about latitudes 40°N and 40°S, closer examination of historic Japanese catch rates clearly shows that the density of the species is very sparse in open-ocean areas, but much more ‘clumped’ near large land masses and continents. In fact, the black marlin is the most land-associated of the billfishes, preferring waters on or near continental shelves during most stages of its life cycle.
Areas where black marlin aggregate include the northern part of the Great Barrier Reef, the east coast and the north-west shelf of Australia, extending to the southern islands of Indonesia, the South China Sea off Vietnam, Malaysia and Thailand, in the eastern Pacific off Peru and Central America (Panama and Ecuador) and off Kenya and Mauritius in the Indian Ocean.

Black marlin do not occur in the Atlantic Ocean; however, Japanese research longliners historically recorded stray black marlin from time to time in the Atlantic as far north as the coast of Brazil and even in the Caribbean. The likely route for these infrequent ‘invasions’ would be around the Cape of Good Hope, and most world distribution maps of black marlin show dotted arrows following this route. Even so, such occurrences are considered very rare.

Most tagging of black marlin by recreational anglers has been undertaken off eastern Australia. The first black marlin was tagged off Cairns, Australia, in 1968 and since then, more than 46,000 black marlin have been tagged off eastern Australia. Of the total tagged, more than 350 recaptures have been recorded, adding...
substantially to our knowledge of this species.

The long-distance movements of some tagged fish give the impression of mass long-distance dispersal of black marlin. However, this picture does not necessarily mean that many or most fish take these routes in all or most years. It does, however, clearly indicate that the species is capable of very extensive movements and that exchange of individuals throughout the species’ Pacific-wide range can and does occur. A study of the genetics of black marlin in the Indo-Pacific confirmed this picture in that no differences could be found between DNA ‘fingerprints’ from fish taken from throughout the black marlin’s range. This finding of apparent widespread mixing indicates that there is almost certainly only one stock of black marlin in the Pacific (quite possibly extending to the Indian Ocean as well). The important implication of this finding is that international cooperation in managing the species needs to be on an ocean-wide scale.

Another question raised by the tagging results is whether the movements of black marlin are random, or part of some purpose-driven migratory cycle. Tagging results clearly show that, after a period of several months, the average distance moved by tagged fish increases rapidly with time at liberty, at least for the first nine months or so after release. This rapid dispersal takes fish away from the tagging grounds off eastern Australia throughout the western Pacific and beyond at an average rate of approximately 20 km per day. (Minimum movement rates of over 60 km per day have been recorded for some recaptured fish, but these have been short-term recaptures and are the exception to the rule.) In addition, the recapture data also show that there is a very marked ‘cluster’ of recaptures near the point(s) of release after about one year (330 to 400 days) followed by another period of apparent rapid dispersal in the ensuing months. Clustering of recaptures near release points is also apparent after two years, and also after three, four and five years (with decreasing numbers of recaptures as time increases). This fascinating finding suggests either that some fish never leave the areas in which they were tagged, or that annual homing occurs, at least for a proportion of the population. Careful examination of Japanese catch data for the Great Barrier Reef over long periods showed that, by early summer each year, catch rates of black marlin suddenly declined dramatically, indicating a sudden en masse departure of fish from that area over a very short time. Long-term charter boat captains in

An adult black marlin photographed off the Great Barrier Reef, Australia. Note the rigid, curved pectoral fin and the relatively low dorsal fins, both characteristics of this species.

Guy Harvey
the area also attest to the fact that black marlin virtually disappear completely at this time, leading to the conclusion from tag returns that at least some fish must be returning to the reef on an annual basis. An important question is, what proportion of the population completes this annual cycle? Perhaps the next generation of high-tech satellite tags will provide the answer.

By analyzing the size ‘pulses’ of small black marlin which appear along the east coast of Australia, it has been estimated that they reach a size of about 25 kg (55 lb) at one year of age, and that a 100 kg (220 lb) fish would be three to four years old. A small sample of very small black marlin have been aged by counting presumed daily rings on their otoliths. Previous work on tuna indicates that these rings are laid down every day during the early life of fish, and assuming that this is also the case for marlin, two 4 kg (9 lb) black marlin were estimated to have been only about 130 days (four months) old when they were caught. A rare, even smaller specimen of a black marlin, only 45 cm in length, was also aged in this way and estimated to be about 80 days old.

After several years of age, the growth rates of black marlin become more difficult to assess, but all evidence so far points to continued rapid growth. It is quite likely (but as yet, unproven) that male black marlin grow more slowly than females and die at an earlier age, explaining why all fish over about 170 kg (375 lb) are females.

The maximum size to which black marlin grow is of the order of 700 kg (1540 lb), the all-tackle world record for the species being 708 kg (1560 lb) for a fish caught off Peru in 1953, while another weighing 691.7 kg (1525 lb) was caught in the same area in 1954. Nearly 600 fish weighing more than 454 kg (1000 lb) have been captured since then, nearly all off Cairns, Australia, but none has exceeded these two long-standing records. There are persistent anecdotes of much larger black marlin being caught by longline vessels, but none of these has ever been substantiated.

Examining the gonads of black marlin caught by both recreational anglers and Japanese longliners, together with some records of occurrence of black marlin larvae, has revealed that spawning takes place in the Coral Sea in late spring/early summer each year. Egg counts from ovaries taken from adult females weighing between 400 kg (880 lb) and 600 kg (1320 lb) ranged from 65 million to 250 million eggs. As is the case for other istiophorids, the frequency of spawning for black marlin is not known.

The fully ripe eggs of the black marlin, about 1.3 mm in diameter, are fer-
tized externally, after which they float at the surface for several days before hatching into tiny larvae. The larvae are themselves miniature predators of the planktonic world – all eyes and mouth, with one purpose – to eat and, therefore, to grow. The mortality rate during these critical early stages must be prodigious, as a whole suite of slightly larger predators take their relentless toll. Although mortality rates are obviously extremely high, it is still difficult to understand why very small black marlin, less than about 10 kg (22 lb), are extremely rare in recreational and commercial catches. It is possible that, during this phase of their life cycle, very small fish remain offshore in the midwater zone, and are therefore not available to most fishing gears, although this explanation obviously needs to be tested.

The vertical behavior of black marlin has been revealed by tracking using ultrasonic tags, as well as by analyzing data from popup satellite tags. In most cases, tagged black marlin tended to swim closer to the surface during the night compared with the day. There is also a tendency for fish to dive to deeper depths after dawn, and to make more ascents to the surface after about noon. Tagged fish rarely penetrated the thermocline, and then only briefly, remaining at temperatures no more than 8°C below that of the surface waters. The deepest dives so far recorded have only been to about 180 metres. During tracking, fish tended to initially move offshore from the edge of reefs before heading parallel to the shore. The average mean swimming speeds over the ground for tracks lasting up to 28 hours ranged from about 1.5 to 4 knots.

Although black marlin are not now targeted by most commercial fisheries in the Pacific, the numbers taken each year as bycatch are quite large. It has been estimated that in the western and central Pacific, at least 30 000 black marlin are taken annually. Beginning in the early 1950s, Japanese longliners consistently fished off northern Queensland, Australia, and during the peak years of the 1960s, up to 14 000 fish were taken annually by that fishery. A long-standing charter fishery for black marlin off the Great Barrier Reef, Australia, has operated successfully for more than 40 years. During that time, strike rates have fluctuated considerably, but the fishery has proven itself to be sustainable over this entire period. Black marlin are also a significant component of a recreational fishery off Panama. In the 1950s, many large black marlin, including the two largest on record, were caught by a small group of anglers operating from a fishing lodge in Peru. The question of whether or not that area still attracts and holds a population of black marlin is one which many would like to answer.
While these arguments imply direct competition between humans and marine animals for the same resources, several important points need to be made. Commercial and recreational catches consist largely of finfish, while the diets of whales, dolphins and seabirds include high proportions of cephalopods (squid and octopus) and crustaceans. Seals certainly target fish, some of which are also caught by people, but they also eat a lot of squid. As well, many of the fishes being consumed by marine mammals and birds are not the same species as those targeted by humans, or if they are, they are not caught at the same sizes. Many of the most abundant species of seabirds, for example, eat very small fishes, or even fish eggs, while it is also known that whales rarely compete directly with humans for the same fish stocks.

So, even though these sorts of simple comparisons don’t tell us a lot about direct competition between humans, fishes and other marine animals, they do help to focus on the connections between human use and the oceanic food web. We know that predation at all levels within the food web has existed in the oceans for eons, and that such predation is the cause of a large component of what is called ‘natural mortality’ of fishes and other marine organisms. The very recent introduction of the human element into ancient food webs is a new and poorly understood additional pressure on these natural systems and it is therefore risky to increase exploitation on already existing large scales before we have a fuller understanding of the whole picture. We can coexist with and within these food webs. We just have to learn more, and take care at every step along the way.