The Ocean Sunfishes

Evolution, Biology and Conservation

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Foreword

As executive director of a public aquarium that's home to more than 500 different species, I probably shouldn't admit that I have a favorite. But I do. It's the ocean sunfish, or *Mola mola*.

As with many marine species, there's much we don't know about these remarkable fishes, despite the fact they've fascinated and enchanted people across the globe for thousands of years. They're a favorite of the Japanese—from their classical art to a contemporary Pokémon character. They were referenced in Roman times by Pliny the Elder, and are respected in Polynesian culture. In California, where Monterey Bay Aquarium is located, they were part of the diet of indigenous people—a conclusion drawn by anthropologists based on abundant *Mola* remains found in 4,000-year-old midden sites on the southern California coast.

Everything about ocean sunfishes is so unlikely, which is perhaps what makes them so oddly endearing. It starts with their half-a-fish body shape and their impressive size (Astonishingly, they increase in size more than 600 million times from their larval state to full maturity, with some individuals growing to weigh 2,300 kg and spanning 3 m from tip to "tail").

It's remarkable to realize they can grow so large when they begin life as tiny plankton, adrift in an ocean filled with hungry mouths. The lucky few that do manage to survive to maturity are the progeny of mothers who can produce hundreds of millions of eggs during their lifespan.

I'm not alone in my fascination for the ocean sunfish. Aquariums in Japan have a long history of featuring *Molidae* in their living exhibits. We sought our colleagues' advice before including ocean sunfish in our Open Sea exhibit when it first opened in 1996. We were (and remain) one of the few aquariums in the United States ever to exhibit *Mola mola*. They have been a consistent favorite with our visitors ever since—although they continue to challenge our animal care team.

Their popularity makes them effective ambassadors for their wild kin in the global ocean. Sharing their story gives us opportunities each day to talk with visitors—two million people a year at the Monterey Bay Aquarium, and three million who connect with us through social media—about how threats to ocean health from climate change, poorly managed fisheries and plastic pollution put ocean sunfish and other marine life at risk.

We've found that the emotional bonds our visitors form with ocean sunfish at the aquarium make them more receptive to learning about threats to ocean health that put wild sunfish at risk—and to ask what they can do to make a difference.

Inspiring people, and connecting them with the story of these impressive fishes, is the impetus for The Ocean Sunfishes: *Evolution, Biology and Conservation*. The book also demonstrates that effective communication begins and ends with rigorous science. You'll find it in abundance in this volume that brings the latest *Molidae* research together in a single place.

Scientific discoveries are advancing at a rapid pace, thanks to new tools and technologies. This book reflects the full scope of what's been learned about these singular fishes. It also highlights questions that science has yet to answer and offers an invitation to new generations of researchers to build on the work of their predecessors. I hope the book inspires students and scientists to keep expanding the knowledge, appreciation and conservation of *Molidae* around the world.

Science and storytelling go hand in hand, and editors Tierney Thys, Graeme Hays and Jonathan Houghton have included an important chapter devoted to the timeless hold ocean sunfish have on our imaginations. I see this every day at the aquarium. Whether *Mola mola* inspire or amuse, entice divers to travel to see them in the wild, prompt TED Talks or disparaging social media diatribes, this is certain: No one is indifferent to these impressive fishes.

I'm confident, based on our experiences at Monterey Bay Aquarium, that we can harness fascination for *Molidae* in ways that will secure a bright future for the living ocean, and for these unlikely charmers. They deserve no less.

November, 2019

Julie Packard
Monterey, California USA

Preface

The oft repeated mantra that "nothing is known about the elusive ocean sunfishes" no longer holds true as evidenced by the wealth of information presented in this book: *The Ocean Sunfishes: Evolution, Biology and Conservation*. When we first began researching these bizarre behemoths, back in the early 1990s in the case of T. Thys, the field of ocean sunfish research was wide open. Very few people, outside of devoted ichthyologists, had ever heard of ocean sunfishes, let alone dedicated substantial time to their study. Decades later, this story has changed dramatically. Interest and explorations into the Molidae as well as many elusive ocean animals, have exploded—a surge fueled, in part, by social media, an insatiably curious, ever-growing human population and crowd-sourced datasets. Each new discovery has been accompanied by an increased scientific appreciation for marine megafauna as individual entities, mobile data-gathering assistants and powerful players in the vast and varied ocean food web.

Our book draws from an impressive worldwide selection of molid researchers with contributors hailing from Australia, Austria, Brazil, Chile, Denmark, Ecuador, Ireland, Italy, Japan, New Zealand, Portugal, Spain, Switzerland, Taiwan, United Kingdom and the USA. This broad geographic distribution of contributors mirrors the circum-global nature of the Molidae themselves who boast a remarkably wide geographic range. Molid sightings span from north of the Arctic Circle off Norway to the Beagle Channel off Ushuaia, Argentina and everywhere in between.

Our book is organized as a journey from the fossil origins of pre-Miocene Molidae through the various aspects of molid life history to the future of molids in an ocean greatly impacted by overfishing and increasing climate pollution. Each chapter ends with a set of remaining questions specific to that area of research. It is our hope that this book will be the go-to resource for anyone with a deep interest in the ocean sunfishes and most importantly as a springboard for future researchers eager to make new discoveries.

The Ocean Sunfishes: Evolution, Biology and Conservation has been a labor of love and a richly collaborative effort. We hope you enjoy reading it as much as we enjoyed putting it together. We extend a special thanks to all the contributors for their excellent research, willingness to join this effort and for being so delightful to work with. We would also like to thank the members of the Molidae family for their limitless capacity to astound, inspire and entice the public and research communities alike to better understand our ocean world. The ocean sunfishes are a wide-eyed reminder that we still have much to learn about our wondrous blue planet.

January 2020

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Tierney M. Thys

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Graeme C. Hays

Thanks to Tierney Thys for very kindly inviting me to be part of this adventure and for her endless enthusiasm and support throughout the gestation of this book. Jonathan Houghton and Tom Doyle for introducing me to ocean sunfish during amazing field-trips on the west coast of Ireland and for the long-term collaborations we have enjoyed, over two decades, looking at the roles of jellyfish as food for marine megafauna.

Jonathan D.R. Houghton

Thank you to Tierney Thys for the very generous offer to co-edit this book with her; Graeme Hays for allowing myself and Tom Doyle to go off on a sunfish tangent during our post-doctoral years; Tom

Doyle for his enthusiasm, intellect and shared propensity to speculate wildly about sunfish after a few pints (to the dismay of Graeme Hays). Thanks Graeme for humoring our early intellectual forays into the unknown; Lukas Kubicek for introducing me to the stunning opportunities the Mediterranean Sea offers for sunfish research and all his help in the field.

G&M Williams Fund for a travel bursary to Tierney Thys to visit Queen's University Marine Laboratory, Portaferry for an editorial retreat. My lab at QUB for keeping the science (and humor) coming during my shift to a more sedentary academic lifestyle. My sunfish collaborators over the years (especially Tom Doyle, Chris Harrod & Natasha Phillips) without whom I would lay no claim to knowing anything about ocean sunfish. And last (but so far from least) my family for keeping me afloat all these years.

Dedication

This book is dedicated to:
Dr. Stephen A. Wainwright a visionary scientist, artist and lover of all anatomical oddities

Nature reveals great secrets in her extreme forms.

Contents

CHAPTER 13

Sunfish on Display

Husbandry of the Ocean Sunfish *Mola mola*

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Introduction

The ocean sunfish, *Mola mola* (Linnaeus 1758), is an odd-looking creature requiring constant vigilance for successful display in public aquariums. While much progress has been made in captive management strategies over recent decades, displaying ocean sunfishes publicly still presents many challenges due to their numerous atypical life history traits. For example, relative to their body size, ocean sunfishes, require an enormous amount of space (ideally hundreds of thousands of liters per animal). Their unusually shaped bodies require careful handling. Despite being encased in a notably thick collagenous underlayer of hypodermis (Bemis et al. 2020 [Chapter 4], Watanabe and Davenport 2020 [Chapter 5]), their external dermis is highly sensitive and wears off easily through excessive contact with enclosure surfaces. Such abrasions can lead to secondary infections. Additionally, their large and rapid growth rates must be kept in check by closely monitoring ontogenetic shifts in dietary needs and adjusting the volume, calories and food composition of the diet. This chapter highlights best practices and guidelines from key institutions that have achieved success in the long-term display of ocean sunfish. It also acknowledges that each sunfish specimen is an individual who will experience unique challenges in its journey through any aquarium program. However, the rewards of presenting such an ocean oddity to the public far outweigh the challenges of captive management.

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The History of Sunfish in Aquariums

The history of ocean sunfish, *Mola mola*, in public aquariums dates to the early 1900s. Suyehiro and Tsutsumi (1973) reported that the New York Aquarium exhibited a 75 kg ocean sunfish as early as 1919 while the Steinhart Aquarium in San Francisco displayed an individual for seven days in 1961, noting the successful delivery of 'clam' as a food item. Arakawa and Masuda (1961) make reference to twenty-one days of rearing data from captive mola at the Miyajima Aquarium, Hiroshima, Japan in 1960. This paper also provides an account of sunfish swimming motion and speed, buoyancy control by way of the hypodermis and eating habits.

Progress towards successful public display of ocean sunfish (here referring primarily to *Mola mola*) steadily increased in Japan in the 1970s (Nishimura et al. 1971, Araga et al. 1973, Tatsuki et al. 1973, Suyehiro and Tsutsumi 1973, Shimoyama and Kawamura 1978). Taking stock of these advancements, Suyehiro and Tsutsumi (1973) reviewed the collection, transport, handling, size and rearing enclosures for ocean sunfish. Based on 47 days of data (the longest recorded tenure at that time) Tatsuki et al. (1973) concurrently examined rearing conditions and captive behavior with reference to swimming speed, suitable water temperature, tank depth and overall utilization and diet. This was one of the earliest accounts of target feeding, with recommendations on the minimum essential feeding rate. Common to all these studies was an effort to understand the species, *Mola mola*, through captive observations and necropsy results. While Shimoyama and Kawamura (1978) reported basic biometric information on the relationship between total length and total height, their main goal was to improve the rearing environment by focusing on water quality which was a unique approach at the time.

In the 1980s, rearing practices for ocean sunfish continued to develop rapidly in Japan. Tsuzaki (1986) and Kondo (1986) described rearing efforts at Kamogawa Sea World, including the first documented use of a transparent polyester film fence to minimize collisions with the enclosure walls. This approach led to significant progress in reared sunfish longevity, with Kamogawa Sea World achieving the world's first year-long tenancy for an individual sunfish in 1979. Japanese aquariums established modern husbandry management practice for the species, providing clear guidance on training and hand feeding by means of a feeding rod (target) and adjustments of feeding rations based on daily observations. Furthermore, they standardized the routine collection of biometric data on reared specimens by recording total length (TL) over time and body mass (BM) based on TL-BM relationships.

This groundbreaking work paved the way for the worldwide aquarium community. In the mid-1980s, public aquariums in the United States including the New Jersey Aquarium on the east coast and Sea World San Diego and Monterey Bay Aquarium (MBA) on the west coast, began working with locally sourced specimens. However, these early rearing efforts outside of Japan resulted only in modest success. For example, MBA's semi-open enclosure system had seasonal drops in water temperature below 13ºC which could not be tolerated long-term by individuals of 40–70 cm TL (Sommer et al. 1989; F. Sommer, personal observations). Nonetheless, this learning curve motivated MBA to consider the needs of ocean sunfish specifically while designing a new exhibit that opened in 1996. Since then, MBA has reared several large specimens (100–200 cm TL), thus far returning more than 20 ocean sunfish back to the wild. Numerous European facilities have also embarked on their own efforts with sunfish in recent decades. In 2000, the North Sea Oceanarium in Denmark landed a sunfish in local waters (an unusual occurrence) and reared it to nearly 300 kg. Since 2002, many other facilities such as the Oceanogràfic de Valéncia in Spain and the Oceanário de Lisboa in Portugal have kept sunfish consistently. Presently, 12 public aquariums worldwide have active ocean sunfish husbandry programs, displaying them to the amazement and delight of the general public (Table 1).

Table 1. List of public aquariums that support active ocean sunfish husbandry programs and commonly display the species, *Mola mola*.

Continent	Country	Aquarium
Asia	Japan	Aqua World Ibaraki Prefectural Oarai Aquarium (Oaraimachi, Ibaraki)
		Ashizuri Kaiyoukan Aquarium (Tosashimizu, Kochi)
		Echizen Matsushima Aquarium (Sakai, Fukui)
		Kamogawa Sea World (Kamogawa, Chiba)
		Osaka Aquarium Kaiyukan (Osaka, Osaka)
		Shima Marineland (Shima, Mei)
		Sunshine Aquarium (Toshima City, Tokyo)
Europe	Denmark	Nordsøen Oceanarium (Hirtshals, Nordjylland)
	Portugal	Oceanário de Lisboa (Lisboa, Estramadura)
	Spain	L'Aquarium de Barcelona (Barcelona, Barcelona)
		Oceanogràfic de Valéncia (Valéncia, Valéncia)
North America	USA	Monterey Bay Aquarium (Monterey, California)

Collection/Acquisition

Ocean sunfishes occur in sub-tropical and temperate zones of the world ocean (Pope et al. 2010, Phillips et al. 2017). The record holding ocean sunfish, caught in Kamogawa, Japan in 1996, measured 2.72 m long and weighed 2,300 kg (see Pope et al. 2010). In 2004, fishers recorded a 3.32 m *M. alexandrini* (Ranzani 1839), near Aji Island, Japan (Sawai et al. 2018), but unfortunately it was not weighed so cannot be confirmed as a record holder. Nevertheless, given their unusual appearance, ability to grow to immense sizes, typically slow, deliberate movements and charismatic nature, ocean sunfishes are highly sought after by large public aquariums.

To that aim, the best way to capture ocean sunfishes depends on location and local regulations. Successful captures and transportation minimizes handling and reduces the impacts of physical contact through the use of vinyl stretchers or hoops, rubberized dip nets, and latex/vinyl gloves. The most common methods of capture include: small scale set nets (Japan), small scale set nets (Mediterranean: Almadraba, Armação, and Tonnarella), purse seines, and targeted dip netting. Permanently anchored set nets off the coast of Japan funnel all incoming fauna into smaller and smaller nets (leader, impounding and bag). The nets are checked routinely (every day or every few days) and the final bag net is pursed by means of several boats working in synchrony. While there is some bycatch using this method, Ishidoya and Ishizaki (1995) report a very low discard ratio. Public aquariums often broker deals with the local set net owners to procure sunfish via this fishery. Sunfish are easily visible as the net is raised and, once restrained, can be hoisted out of the water and placed into a live well (Fig. 1).

In the Mediterranean Sea, set nets of a slightly different design are employed. Developed to capture tuna during their spawning migrations, they function by running a barrier net from shore to a large catch net with several opposing, angled box barrier nets that lead fish into the final catch net. These are known as Almadrabas in Spain (García Vargas and Florido del Corral 2007), Armação in Portugal (Batista and Gonçalves 2017) and Tonnarella in Italy (Di Natale 2014).

Ocean sunfish often constitute substantial bycatch from these nets, which is either released (i.e., the Italian Tonarella) or sold at local markets. As in Japan, local aquariums, researchers (e.g., Phillips et al. 2018) and collection firms arrange with fishers to collect healthy sunfish. Likewise, Peniche on the west coast of Portugal, hosts multiple commercial seine fishing companies that target *Sardina pilchardus*, *Scomber* spp. and *Trachurus trachurus*. Local fishermen report that *Mola mola* never

Figure 1. Large ocean sunfish being lifted from set net for satellite tagging. Chiba, Japan. Photo taken and permission granted by: Michael J. Howard.

occur during *Sardina pilchardus* hauls but are common when *Scomber* spp. are prevalent (P. Leitão, personal communication). This purse seining fleet has served as another source of sunfish since 2017.

In the United States, where set nets are banned, sunfish are targeted individually. This method requires calm waters with little to no breeze so that collectors can spot sunfish fins when they break the surface. The presence of cetaceans or sea lions typically frighten sunfish away (M. Howard, personal observations). Gulls sitting on the sea surface and/or pecking into the water (e.g., Western gulls, *Larus occidentalis*, and Heermann's gulls, *L. heermanni*) can signal a sunfish's presence as they are known to remove ectoparasites from sunfish at the surface (Tibby 1936, King 1978). Similar observations are reported for Laysan albatrosses, *Phoebastria immutabilis*, from coastal waters off Japan (Abe et al. 2012). When a sunfish is engaged with a gull that is picking parasites, it is focused on that activity and usually much easier to capture than free-swimming sunfish. A spotter plane may also be used to help locate individuals, but this greatly increases the costs of capture. As drone technology continues to improve, it is likely that this technology will come into play increasingly.

Swimming individuals are difficult to net and require a fast ambush approach. Alternatively, animals that are basking or being cleaned are better approached slowly and captured with a rapid thrust of the net into the water to secure the front of the fish. In all cases, a rubber net is employed, and the fish is lifted out of the water immediately to restrain it under its own weight. This approach prevents fin tips from entangling in the net by minimizing fin movement. The fish can then be placed immediately into a live well on the vessel, with fin tips protected at all times during capture and transport.

Transportation

Short Distance, By Sea or Land

Like the targeted sunfish, those caught in the set-nets and purse-seine nets should be removed carefully from the water using non-abrasive vinyl stretchers or rubber nets, operated by aquarists wearing latex gloves to minimize the removal of mucous and damage to the epidermis. Once on a fishing vessel, there are several transportation methods available to reduce fish movement and minimize contact with tank walls. One option maintains sunfish in a tank with a sealed combing lid top which eliminates the sloshing of water; this, combined with dissolved oxygen (DO) levels maintained at 120–150 percent, calms the fish and reduces overall movement during transportation. In this case, sunfish usually stay at the bottom of the tank and move very little. Another option carries sunfish in a free standing, tall, circular tank (fiberglass or polyethylene) with a significant (40–50 cm) air gap between water line and tank lid. As sloshing occurs during transportation, causing some fish movement, the air gap should be great enough to prevent dorsal fin contact with the top of the tank. Transportation in Portugal and Spain is based on round polyethylene tanks (1.4–1.6 m diameter) filled to a depth of 0.8–0.9 m of natural seawater. Transit times are typically one to two hours during which DO levels are maintained above 100 percent saturation to help keep the fish relaxed and still. For the Peniche collections, Betadine® (10 percent povidone-iodine) is added to the transportation water, at a concentration of 10 ml/m^3 to serve as a prophylactic antiseptic treatment to address any minor damage to the dermis incurred during capture (from purse seine netting and handling).

Long Distance, By Land and Air

Long distance transportation presents additional challenges. It should not exceed 45 hours and must align with well-established welfare protocols for the physiological and operational aspects involved during such transportation (Smith 1992, Correia 2001, Young et al. 2002, Smith et al. 2004, Correia et al. 2011, Rodrigues et al. 2013, Correia and Rodrigues 2017). Correia et al. (2008) provide specific details on the transport of *Mola mola* (although the methods described by those authors have been modified since airlines have banned the inflight use of lithium batteries and compressed oxygen). Due to dimensional limits to cargo transportation tanks, sunfish designated for shipping should be small (< 50 cm TL). Other concerns for shipments lasting more than two hours include: (1) a gradual decrease in pH, (2) elevated levels of ammonia, and (3) a steady decline in DO which occurs from the build-up of carbon dioxide, nitrogenous waste and stress-related metabolites, and through consumption of DO by means of respiration. These three issues can be addressed through water filtration and the addition of chemical supplements and oxygen. Likewise, the control of pH can be achieved via buffering agents such as common baking soda (sodium bicarbonate, $NaHCO_3$) or soda ash (sodium carbonate, Na_2CO_3). Ammonia (NH_3 and NH_4^+) can be removed with the assistance of quenching agents such as AmQuel® ($HOCH_2SO_3$) (Novalek Inc., U.S.A.), which binds to ammonia and transforms it into non-toxic aminomethanesulfonate ($H_2NCH_2SO_3^-$) and water. This substance has been used successfully in the transportation of marine species for many years (Visser 1996, Young et al. 2002, Smith et al. 2004, Correia et al. 2008, 2011, Rodrigues et al. 2013, Correia and Rodrigues 2017). The decrease in oxygen saturation rate, a direct result of respiration, may be counteracted by supplying oxygen through the use of an air-stone connected to a cylinder of compressed medical grade oxygen.

Post-capture, all candidates for long distance transportation should first receive a gross physical examination to assess condition. When deemed 'healthy' and in an unstressed state (i.e., orienting well within the enclosure and displaying appropriate targeting and feeding responses) all animals should be fasted for two days before transportation to limit the build-up of nitrogenous waste during transit. Transportation details for several successful efforts are listed in Table 2, and shown in Figs. 2, 3 and 4.

Figure 3 shows transportation tanks ready to be loaded onto a plane. They are 1.4 m diameter × 0.9 m high, filled with 0.7 m of seawater, creating a usable volume of 1.1 m^3 to accommodate one or two four kg sunfish, which equates to a bioload (i.e., the amount of living matter in a tank) of either 3.6 or 7.3 kg/m^3 (Table 2). Table 2 illustrates how various water volumes and bioloads can achieve successful transportation as long as the water is buffered properly, and adequate nitrogen quenching agents are employed. To achieve the most stable water quality, 50 g of sodium bicarbonate and 50 g of sodium carbonate are added to the oxygenated water along with 10 g of AmQuel® which lowers pH. Like other teleosts, ocean sunfish remain practically motionless in this type of transit. The addition of AmQuel® coupled with pH buffering agents contributes significantly to the successful delivery of these fish. In the absence of buffering agents, the water chemistry degrades to lethal levels.

Tanks shipped via air cargo are subject to strict rules and inspected thoroughly by airport officials. It is important to use a fiberglass reinforced lid bolted to the polyethylene tank to ensure a leak-proof seal. A Plexiglas® hatch allows for visual inspections of the animals, including their positioning within

Table 2. Operational specifications for *Mola mola* transport using tanks fitted with filtration (up to 2010) and sealed, with no filtration (2014–present) to multiple international destinations. Transportation with O_2 fed continuously targets 150 percent saturation. All other transports involve tanks fed with oxygen until delivery to the airport, approximately four hours before each flight, at which point the tank is sealed with 300 percent saturation and oxygen supply is discontinued.

Date	No. Fish	Indiv. Weight (kg)	Destination	No. Fish/Tank	Tank Dimensions (Diam. x Height, m)	Volume (L)	Bioload (kg/m^3)	Duration (hr.)	Transport	O_2 on arrival (%)	Survivorship in Transit	Introduction	Survivorship after Delivery (days)	Necropsy
05/04/2007	4	4	Atlanta, USA	1	1.4 x 1.1	1100	3.6	43	Road & Air	O_2 continuously	100%	Quarantine	Approx. 14	
11/09/2008	4	4	Dubai, UAE	2	1.4 x 1.1	1100	7.3	44	Road & Air	O_2 continuously	100%	Quarantine	Approx. 14	
05/06/2010	2	4	Stralsund, Germany	1	1.6 x 1.06	1400	2.9	24	Road & Air	O_2 continuously	100%	Main exhibit		Liver damage (parasites); Bacterial infection; Construction may have disturbed
13/05/2014	4	4	Singapore, Singapore	2	1.4 x 1.1	1100	7.3	50	Road & Air	~80	75%	Quarantine	Approx. 14	
01/07/2014	2	3	Hirtshaals, Denmark	2	1.35 x 0.9	540	11.1	17	Road & Air	~60	100%	Main exhibit	5 years + est. 500 kg & alive at time of publishing); 2.1 years (euthanized at 168 kg due to severe lesions)	
11/07/2014	1	3	Copenhagen, Denmark	1	1.35 x 0.9	617	4.9	12	Road & Air	~80	100%	Quarantine	a few days; approx. 30 days	Heavy parasite load in gills and liver
13/08/2014	1	5	Copenhagen, Denmark	1	1.35 x 0.9	500	10.0	12	Road & Air	~80	100%	Quarantine		
11/05/2017	1	4	Moscow, Russia	1	1.4 x 0.9	700	5.7	16	Road & Air	~80	100%	Quarantine	11 days	Internal parasites; Multiple organ failure
16/10/2017	2	4	Boulogne-Sur-Mer	2	2.4 x 1.0	3600	2.2	30	Road & Air	O_2 continuously	100%	Main exhibit	3 days; 5 days	
20/10/2017	2	4	Dubai, UAE	1	1.2 x 1.2	700	5.7	16	Road & Air	~150	100%	Quarantine	1 day; 2 days	
30/05/2018	1	4	Hirtshaals, Denmark	1	1.4 x 0.9	750	5.3	17	Road & Air	~100	100%	Quarantine	1+ years (alive at time of publishing)	

Figure 2. Polyethylene transport tank used for *Mola mola*: (1.4 m diam. × 0.92 m high) with 750 L capacity. The tank flies completely sealed, (IATA LAR 60) with a small aeration unit mounted under the lid. The unit dissolves oxygen that was added previously into the water. The water level is approximately half of the height. Photo taken and permission granted by: João Correia, Flying Sharks.

Figure 3. Four tanks loaded with one *Mola mola* each at JFK airport on the 5th of April 2007, en route to Georgia Aquarium, in Atlanta, USA. Each tank is loaded with 1100 L of seawater and one four kg animal, yielding a bioload of 3.6 kg/m^3. Total transit time was 43 hours and all animals arrived alive to their destination. Each tank was equipped with a 12 V bilge pump and was fed continuously with oxygen, for a target saturation of 200 percent. Photo taken and permission granted by: João Correia, Flying Sharks.

Figure 4. SCUBA diver hand feeding ocean sunfish, *Mola mola*, at the North Sea Oceanarium, Denmark, taken in the spring of 2019, with an estimated mass of over 500 kg. The specimen was originally shipped via air cargo in July, 2014 (see Table 2). Photo taken and granted permission by: North Sea Oceanarium.

the tank. As a rule, whenever aquarists have access to the transportation tanks, they should check the system and animals at regular intervals. Checks should include the animal's behavior and respiration rate, equipment functionality and water quality parameters, such as temperature and DO (using, for example, a hand held OxyGuard® Handy Oxygen probe®—OxyGuard Intl., Denmark), pH (using, for example, a hand held OxyGuard® Handy pH® probe) and ammonia (using, for example, Tetra® Ammonia test kits—Tetra Werke, Germany).

Current aeronautical regulations require the use of completely self-contained, sealed tanks. The sealed tanks contain only seawater, the animal, and a small, three V aeration unit (mounted on the lid underside) to dissolve pure oxygen into the water. Water is exchanged by 70–80 percent approximately 30 minutes after the animals are placed in the tanks before driving to the airport. Oxygen should be administered continuously while travelling. Both pH and ammonia buffering agents are used to keep parameters stable and, in the case of pH, above normal before sealing the lid (to account for gradual decline during shipment). Arrangements should be made with ground handling agents at the airport to ensure access to the shipping containers until the last possible moment before the actual loading of the aircraft, at which point final measurements of oxygen, pH and ammonia are made, and buffering agents can be applied as needed. DO should be raised to 300 percent to supply enough DO for the sunfish on the flight, during which supplemental oxygen cannot be administered after sealing the lid with silicone. When transportation containers arrive at the destination, all animals need to be acclimated to the system water of their new enclosure. All sunfish (previously target trained and having fasted for two days prior to shipment) should be offered food as soon as possible using their targets as a cue in order to resume the target training process. Figure 4 shows a sunfish on exhibit at North Sea Oceanarium five years after being shipped using these methods.

Despite such precautions, mortalities during transportation do occur. Necropsy data from sunfish that do not survive long term post-delivery usually reveal moderate to heavy internal parasite loads, particularly in the liver and/or systemic bacterial infection. It is difficult to know if such infections were present prior to transportation or as a result of sustained stress once at the receiving institution. Blood sample analyses pre and post transportation may provide greater insight during future efforts. Marked shifts in water temperature between capture sites and quarantine/exhibition tanks should be avoided where possible.

Accession/Training/Quarantine

Even for small sunfish (< 50 cm TL), water volume and depth in particular (> 150 cm) are extremely important for individuals to thrive during quarantine. It is also good practice to include a soft vinyl curtain that hangs loosely, a set distance away from the hard sides of the enclosure to reduce abrasion while the individual progresses through quarantine and training. The quarantine enclosure should be as large as possible, ranging from 3.5–10 m in diameter and 0.8–2 m in depth. To avoid the need for lengthy temperature acclimations, the holding enclosure should match (within 1–2ºC) the sea surface temperature at the point of capture. Throughout the quarantine and training period, the temperature can be increased up to 22ºC (or set to match the destination enclosure's temperature) over the course of several days. All closed systems should employ some form of mechanical and biological filtration components in addition to temperature control. When a semi-enclosed system is used, flow rates must not exceed the chilling or heating capacity to maintain stable temperatures. DO (90–100 percent) and pH (7.7–8.2) levels should be maintained close to normal ocean surface levels.

Successful sunfish display programs do not follow a traditional marine fish quarantine process (which typically involves treatment periods of weeks) as the risk of mortality scales with time. Subsequently, any prophylactic treatments for sunfish should be minimal (oral medications are preferable to injections), usually of short duration (immersion baths in the minutes as opposed to days or weeks) and be as unobtrusive as possible when physical handling is required. Sunfish quarantine is largely an observational period while the fish is target trained. Aquarists need to assess and monitor enclosure utilization, swimming behaviors, respiration rate, gross physical condition (especially the eyes and dermis) and inter and intra-species interactions.

All sunfish should receive an initial health assessment while being accessioned into an aquarium collection or placed into a quarantine enclosure, with all ectoparasites removed at this stage (e.g., via a five-minute freshwater immersion bath, where pH and alkalinity match the transportation water). If the sunfish is visibly distressed in the freshwater bath, ectoparasites can be removed manually by: (1) supporting the sunfish on a round vinyl stretcher just below the water surface of the transportation tank to allow normal respiration; (2) increasing the DO level to 120–150 percent; (3) placing a soft chamois cloth over the upwards facing eye to keep the fish in a 'relaxed' state; (4) using hard plastic forceps, remove all external parasites as quickly as possible. A steady hand is required to avoid scratching the dermis or disrupting the mucous layer. While the sunfish is in this position, basic morphometric information should be recorded using a soft vinyl measuring tape. After the ectoparasites have been removed from both sides of the fish, attach the vinyl stretcher to a digital scale. Briefly lift the fish and stretcher from the water and record the mass once all of the water has drained out. Be sure to record the wet mass of the stretcher, bridle and chamois separately and deduct from gross weight to obtain the sunfish's actual mass. This value can be used to determine an initial dose of oral Praziquantel, an antihelmintic (dosage—12 mg/kg at 56.8 mg/ml). Once all notes on gross physical condition are recorded, introduce the sunfish to the holding enclosure and offer food.

Once in the holding enclosure, the sunfish can be offered 3–10 percent body weight (BW) per day of solid foods (mollusc or crustacean) cut into appropriately sized pieces. Gelatin capsules filled with the appropriate dosage of liquid oral Praziquantel can be implanted into food items and administered at this time. If rejected, food items can be recaptured and offered again until consumed. This process of initially associating food with a visual 'target' is sufficient for the first day, after which the individual should be left to acclimate to its new surroundings until the following day, when the training process can begin in earnest (Fig. 5).

Target training is best performed when sunfish are placed into a holding enclosure by themselves to avoid inter-specific competition. However, this is not always possible, and it is helpful that they eventually have 'tank-mates' prior to any introduction to a display enclosure (discussed later). For simplicity, we describe the process of training one fish at a time. However, because small sunfish (< 60 cm TL) often travel in small schools in the ocean, they should be kept in small groups within aquarium enclosures (whenever possible), from an animal welfare perspective. Starting with feeding, it can be difficult to deliver food to an untrained sunfish in large initial holding enclosures (up to 10 m diameter). Therefore, a visual target (occasionally coupled with a specific audio cue) and hand feeding at stations are critical components to successful sunfish husbandry. Feeding at stations via target training serves many purposes. Primarily, it allows aquarists to deliver a set amount (percent BW per day) of specific food items (Kcal/kg * day) and minimizes 'free-feeding' (which can lead to obesity) or stealing of other food items designated for other animals. It also provides multiple

Figure 5. Target feeding at Monterey Bay Aquarium, 7 September 2016 using a green ball. Photo taken and permission granted by Lawrence Eagling.

daily opportunities for close inspection of body condition and behavior and assists with medication delivery. Finally, target feeding (often delivered at a set 'station') serves as a great enrichment tool.

After accession, the training process usually begins with the target deployed at the start of each training session. As long as the target is distinctly different from any other species-specific targets used within the same enclosure it should be effective. If the sunfish does not respond by swimming towards the target, food can be delivered by means of attaching a piece to the end of a long pole. Since sunfish are surprisingly agile and can swim backwards away from unknown foreign objects, it is important to present food initially from a known blind spot along the dorsal ridge and above its eyes (see Kino et al. 2009) so that the piece arrives smoothly at its mouth and drawn in before it can retreat. If the first few tries are unsuccessful and the fish reacts negatively by swimming away from the food/pole, attempts should cease, and the session should end by removing the target. However, after a few successful deliveries, sunfish swim directly to the food. As this happens, each offering should occur closer and closer to the target so that the association is made. Early in the process, there should be several sessions provided per day (up to six, as time allows) to reinforce the behavior, but the total amount of food offered daily should not exceed its prescribed daily ration by a significant amount. Once a sunfish is routinely targeting and stationing for food, sessions per day can be reduced. Two to three is ideal in order to continue the reinforcement of the training process while dividing its daily rations into more manageable, smaller meals. If at this point the fish appears well acclimatized to its surroundings, it is time to introduce other species as 'tank-mates' into the quarantine enclosure. Allowing an individual to become accustomed to other fish is important, especially in the case of fast-swimming, schooling species that will occupy the same areas within the display enclosure.

A healthy sunfish that has been impacted minimally by the processes of capture, transport and accession should pick up target training in as little as a one day, but for reasons that are unclear, it can take as many as 14 days or more (Monterey Bay Aquarium unpublished data). Force feeding of the sunfish is required in this case. While the training time for some sunfish may be relatively lengthy, their ability to learn target training is quite remarkable, particularly considering its reduced brain size (Chanet et al. 2012). Once a sunfish is well adapted and target trained, it should be transferred to the display enclosure. The process may cause some stress to the individual resulting in a temporary cessation of targeting behaviors (temporarily increasing its daily rations up to a week in advance of a transfer can mitigate the stress from a short-term disruption in food intake). Likewise, in a new and larger display enclosure, a sunfish may simply not know where to find its target. In this case, it may be necessary to deliver food via SCUBA divers. While approaching the sunfish, the dive team should deploy its target while offering food to the sunfish. Over time these targets will facilitate a response without the dive team, usually over a period of two to eight days.

Display Enclosure Styles/Concepts

There are three main styles of display enclosures that have been used successfully for exhibiting the ocean sunfish at public aquariums. Each approach has advantages and challenges, but all follow a similar regime to maintain water quality parameters. The first style, prevalent in Japan, houses sunfish singularly or in small groups within a large, single species display enclosure. These typically are devoid of any reef structure or elements of aquarium décor (e.g., pier pilings, shipwrecks) and are lined with a soft, clear protective vinyl curtain to minimize abrasions. However, curtains also create additional surfaces for aquarists to keep clean and free from diatoms and other algae and their presence is often troublesome to other fishes. However, there are a handful of species, primarily smaller schooling types (e.g., Japanese butterfish, *Psenopsis anomala*) or small juvenile fish that associate with floating material (e.g., blacksmith, *Chromis punctipinnis*, rockfish, *Sebastes* spp.) that can be displayed safely with sunfish in this manner. The second style of display enclosure is a multi-species, sub-tropical, open ocean display which has been used successfully in aquariums in the United States. Notably, there are no structures (natural or foreign) within the display. In the absence of a clear curtain and with no discernable reef structures for orientation, it is essential to monitor enclosure utilization (wall avoidance, especially) and negative interactions with other species (e.g., sea turtles, elasmobranchs). The final approach, used widely in European aquariums, is a multi-species, sub-tropical outer reef habitat. In this type of display, the species list usually includes several different teleosts and large elasmobranchs and occasionally sea turtles. These tanks typically comprise a combination of open spaces along with patches of low-lying reef or habitat structures. This set-up provides an excellent mixture of large open water space for midwater and near surface swimming while also providing spatial context for the sunfish to navigate within the water column and during time spent closer to the bottom and near structures. However, an agitated sunfish may make incidental contact with reef structures incurring injury to fin tips, flanks, eyes, or mouth.

Whatever the enclosure type, sunfish should be maintained in aquariums with water temperatures ranging between 16.5–22ºC. They can be exposed to natural or artificial light with different photoperiods (from 7 to 17 hours of light) with salinity ranging from 32.8–34.5 ppt. DO levels should be maintained between 6.9–7.2 mg/l or 96–100 percent. Sunfish have been known to react poorly when DO levels drop suddenly or are consistently at levels below 90 percent for long durations, suggesting a lack of efficiency in gas exchange through the gills which are notably pale in healthy, living specimens (M. Howard, personal observations). Likewise, sunfish should not be held in aquarium systems that have poorly functioning nitrogen fixing bacteria or incompletely cycled systems. Other dissolved gases (i.e., $NH^3/NO^2/NO^3$) should be maintained at typically acceptable levels for well-run marine systems (0/0–0.005/< 80 mg/l respectively).

Feeding Strategies

New insights from wild sunfish diet research are helping to guide captive practices as well. Recent studies show that wild juveniles consume a rich, primarily benthic diet and, as they grow through sub-adult to adulthood, transition to a diet composed increasingly of gelatinous taxa (Syväranta et al. 2012, Nakamura and Sato 2014, Sousa et al. 2016, Phillips et al. in press). It has been hypothesized (Sousa et al. 2020 [Chapter 8]) that small individuals are more vulnerable to predation and may require food that is richer in order to grow more rapidly and reduce the number of potential predators. However, a closer look at the bioenergetics of different size classes of sunfish through experimental trials within a mega-flume might shed light on the drivers of this dietary shift further (Payne et al. 2015). Replicating this mixed diet under captive conditions is achieved through gelatin-based foods (e.g., agar or low calorie #5BOQ gelatin—Mazuri Exotic Animal Nutrition, Land O' Lakes, Inc., USA) with high water content (60–96 percent) prepared on site. These designed gelatins often include a small portion of molluscan, crustacean, or fish-based material to improve palatability. In turn, such feeds can be supplemented by multivitamins, or additional amino acids and vitamin C to enhance nutritional value. Foods with high water content also help mitigate the risk of dehydration (evidenced by the appearance of wrinkles and/or a shift from moist, slippery mucous to dense, sticky mucous) which can occur quickly (i.e., in less than one day for sunfish < 50 cm TL). Such problems can occur if an individual misses a scheduled feeding event, but can be rectified quickly by providing additional feeding sessions (either at station or via SCUBA) with increased amounts of gelatinous items, liquidized mollusc tissue, or in severe cases, deionized freshwater poured directly into the fish's mouth (Fig. 6).

Further studies are needed to better understand appropriate consumption rates. Living in a stable aquarium environment with fewer metabolic challenges heightens differences between wild and captive food consumption as well as growth rates. Along with daily volumetric intake in percent BW per day, Monterey Bay Aquarium staff also track consumption in terms of Kcal/kg * day. The caloric needs of sunfish decrease with growth and age, making it important to adjust this value over time to prevent obesity. Figure 7 highlights the variability of consumption in Kcal/kg * day for one specimen at MBA, when it has the opportunity to feed freely as compared to days it was fed via targeted session.

Figure 6. Pouring bottled freshwater into a *Mola mola's* mouth to correct dehydration. Photo taken and permission granted by: João Correia, Flying Sharks.

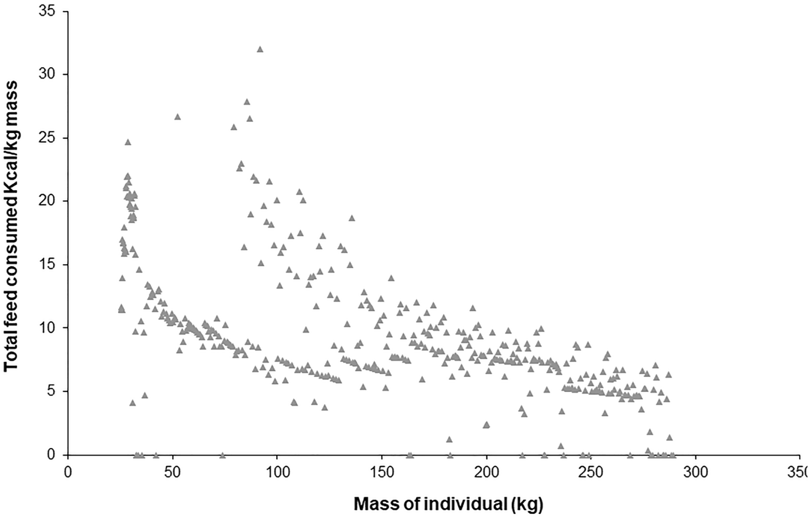

Figure 7. Kcal/kg * day consumption of one ocean sunfish over time at Monterey Bay Aquarium, showing the difference between targeted consumption (daily ration) versus estimated total daily consumption through observed free-feeding of market squids during other animals' feeding sessions. To estimate the additional Kcals consumed, individual squids were weighed, and a standard error curve was applied to ensure the sample size was adequate in relation to the deviation around the calculated mean.

Shortly after it was introduced to the exhibit enclosure, it began to free feed on market squids (*Doryteuthis opalescens*) during the broadcasted tuna feedings. At times, the sunfish was consuming three to four times the amount intended on a daily basis, potentially causing gastrointestinal stress and an obesity issue. As a result of these data, the management strategy was changed to offer two target feeding sessions per day, one of which corresponded with the tuna feedings. This allowed aquarists to keep the sunfish at station to eat its own food (prescribed daily ration) and not the tunas' food.

Understanding natural growth rates of a species in the wild is vital when designing an appropriate captive feeding regime. For ocean sunfish, length/weight data is available from Nakatsubo et al. (2007) and Kamogawa Sea World (Japan) and North Sea Oceanarium (Denmark) (previously unpublished data from North Sea bycatch) (Table 3; Fig. 8). With sufficient singular data points from wild specimens, a general guideline for captive weight management may materialize (Table 4). Nonetheless, more work is required across regions so that generalizable relationships with representative confidence intervals can be generated. A mark-recapture study underway by MBA will help towards this goal, with identifiable individuals measured and weighed over time allowing natural growth rates to be estimated.

Table 3. Average length-mass ratios for wild ocean sunfish from the western Pacific used by permission from Hiroshi Katsumata, Kamogawa Sea World.

Length (cm)	Weight (kg)
40	3.5
45	5
50	7
55	9.5
60	12
65	15
70	18
75	21
80	26
85	32
90	38
95	45
100	52
105	60
110	70
115	80
120	90
125	100
130	120
135	130
140	150
145	160
150	170
155	190
160	210
165	230
170	250
175	270
180	290
185	310
190	340
195	360
200	390

Clearly, data are required from a number of individuals (Cailliet et al. 1992) before relationships can be derived but the effort is far superseded by the potential benefits for refining sunfish husbandry.

Medical Procedures

Medical attention is required for external injuries and behavioral issues. Typical external injuries include dermal abrasions, damage to fin tips, corneal edemas/ulcers, and inflammation or damage to the mouth or jaws. Behavioral indicators of poor health include changes in appetite, stereotypic behavior, disorientation and reduced enclosure usage. When medical procedures are necessary, nitrile or latex gloves should always be worn, handling should be kept to a minimum, and when possible, the fish should remain in seawater to reduce stress and physical abrasion. For minimally invasive treatments, it is helpful to coax sunfish into a 'basking' position at the surface (Abe et al. 2012, Nakamura et al. 2015) prior to treatment to reduce handling stress. However, some procedures require physical restraint. Resting the fish on a vinyl stretcher just above the water, while providing

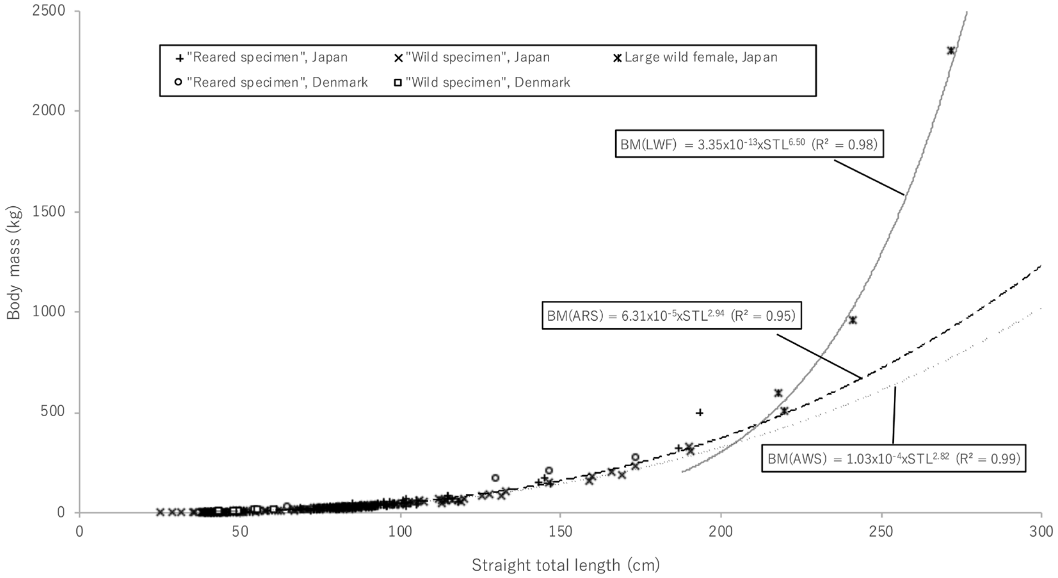

Figure 8. Relationships between straight total length and body mass of ocean sunfish, Mola mola. Solid, dashed, and dotted lines indicate regressions of large wild females (LWF), all reared specimens (ARS), and all wild specimens (AWS), respectively.

Table 4. Conversion table total length to body mass for the ocean sunfish, *Mola mola*, used by permission from Hiroshi Katsumata, Kamogawa Sea World.

Conversion table total length to body weight of ocean sunfish										
	First digit of total length (cm)									
Total length rounded off the first digit (cm)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
0	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.03
10	0.04	0.05	0.07	0.09	0.11	0.14	0.17	0.20	0.24	0.28
20	0.33	0.39	0.45	0.52	0.59	0.67	0.75	0.85	0.95	1.06
30	1.18	1.30	1.44	1.58	1.74	1.90	2.08	2.26	2.46	2.66
40	2.88	3.11	3.35	3.61	3.87	4.16	4.45	4.76	5.08	5.42
50	5.77	6.13	6.51	6.91	7.33	7.76	8.20	8.67	9.15	9.65
60	10.2	10.7	11.3	11.8	12.4	13.0	13.7	14.3	15.0	15.7
70	16.4	17.2	17.9	18.7	19.5	20.3	21.2	22.1	23.0	23.9
80	24.9	25.9	26.9	27.9	28.9	30.0	31.1	32.3	33.5	34.7
90	35.9	37.1	38.4	39.7	41.1	42.4	43.9	45.3	46.8	48.3
100	49.8	51.4	53.0	54.6	56.2	57.9	59.7	61.4	63.3	65.1
110	67.0	68.9	70.8	72.8	74.8	76.9	79.0	81.1	83.3	85.5
120	87.8	90.1	92.4	94.8	97.2	99.7	102.2	104.7	107.3	109.9
130	112.6	115.3	118.1	120.9	123.7	126.6	129.5	132.5	135.6	138.6
140	141.8	144.9	148.2	151.4	154.7	158.1	161.5	165.0	168.5	172.1
150	175.7	179.4	183.1	186.9	190.7	194.6	198.5	202.5	206.5	210.6
160	214.8	219.0	223.2	227.5	231.9	236.3	240.8	245.3	249.9	254.6
170	259.3	264.1	268.9	273.8	278.8	283.8	288.8	294.0	299.2	304.4
180	309.8	315.1	320.6	326.1	331.7	337.3	343.0	348.8	354.6	360.5
190	366.5	372.5	378.6	384.8	391.0	397.3	403.7	410.1	416.6	423.2
	Converted body weight (kg)									
	Converted by the TL-BW formula: $BW=3\times10^{-5}\times TL^{3.11}$									

Figure 9. Using a vinyl stretcher with eye covering and water flowing into mouth and across gills in order to provide an exam. Photo taken and used with permission by: Michael J. Howard.

a flow of seawater into its mouth and through the gill areas can be an effective means of restraint (Fig. 9). Its eye is covered, and water is directed into its mouth (visible gill pumping can be seen as splashes of water coming from the gill opening). In such cases, it is important to cover the eye with a soft chamois and to saturate the respiration water to oxygen levels of 120–150 percent to subdue the fish, minimizing fin movements and reducing stress. This type of restraint provides excellent access to all caregivers and can be employed safely for up to ten minutes on sunfish < 100 cm TL.

Treatments

All treatments should be prescribed by a professional, licensed veterinarian. Superficial abrasions along the flanks or other parts of the body usually heal without treatment. However, when these occur during capture, initial handling, or transport and the sunfish is small, an immersion bath containing 0.1 mg/L of povidone-iodine ten percent (one percent available iodine, commercial name Betadine™) may prove effective in reducing infection. An entire system may be treated for 48 hours, then flushed to allow a sunfish to rest in untreated water for 24 hours. A second 24 h bath of Betadine™, using the same concentration, following the 24 h rest period may be necessary. This course of treatment can be administered once per week and repeated two or three times until all abrasions are healed. While treating an entire system imposes less stress on a sunfish (no handling, provides ample space) the amount, cost, and proper disposal of any therapeutic must be considered prior to implementation. Larger or more significant abrasions can be treated with topical ointments. Gentocil™ (based on the antibiotic, gentomicin) can be effective when combined with Betadine™ for wounds along the body and eyes and can heal lesions within three to four days. Regranex™ is also effective in this context. Most ointments are water soluble, however, which means they may need to be reapplied frequently, especially on high motion surfaces such as fin tips.

Antibiotics can help manage wounds, subsequent infections, abscesses and other growths that may occur along the fin tips due to excessive or repetitive contact with enclosure surfaces. They can also help healing after debridings, amputations and wound closure. These medicines are best administered orally since no handling is required, but this tactic requires the animal to be regularly feeding at station. Enroflaxacin is a helpful oral antibiotic that does not affect appetite. Antibiotics can also be administered intra-muscularly, although this requires additional handling and can add unwanted stress. This technique is typically used with Cefazolin, dosed at 30 mg/kg, and administered in three-day intervals for a total of five injections.

Lastly, when a sunfish's appetite is suppressed, assisted feeding is necessary while the root cause is determined. If there is no obvious cause such as a physical injury or environmental stressors relating to poor water quality, the possibility of inter- or intra-species interactions should be evaluated. If a cause is still not immediately evident, oxolinic acid, a quinolone antibiotic, may be used to stimulate appetite. However, since it is administered orally (12–20 mg/kg for 5–10 days) challenges may arise in delivery, and additional handling may be necessary.

Deaccession and Release

Public aquariums and animal research facilities should have deaccession plans (a disposition decision tree) in place for their specimens prior to the implementation of any acquisition plan. For many animals held in aquariums, husbandry management plans have evolved and advanced to the point at which an acquired specimen will live out a full and enriched life as a species ambassador. For others, including the ocean sunfish, *Mola mola*, this sometimes is not a possibility. This may be due to its growth rate and maximum size (enclosure/transport size limitations), species compatibility (inter and intra-specific), atypical feeding ecology (high volume/low caloric needs), and occasional behavioral issues. At this point, geography can pose a significant challenge as the display facility may be land-locked or located beyond the natural range of the species. In these cases, when release is not possible and quality of life has declined, euthanasia may be the only option as long as it is coupled with a thorough necropsy, sampling and data collection plan. Euthanasia is justified following several considerations. First, this species is an iconic, charismatic animal that holds intrinsic value as an ambassador that will fascinate and educate the public. Throughout a specimen's tenure, the public can learn a multitude of important topics relating both specifically and generally to the sunfish. These include evolution, biomechanics, ecology, bio-toxins, parasites, fisheries and conservation issues (as discussed throughout this book).

With recent advances in animal transportation, it is also possible to de-access animals via institutional trading, with size limitations. This is a good option when access to wild specimens is disrupted through natural disasters or other institutional limitations. The best option, although the most challenging, is a well-designed release plan. However, the path from display enclosure to ocean is a multi-step procedure (Monterey Bay Aquarium, unpublished data) and may require special permission from local authorities. Moreover, the process to move much larger specimens requires the use of SCUBA divers, industrial hoists, specialized restraining devices, and larger transportation tanks on bigger vessels. At no point during the process should the sunfish be without water flowing across its gills for more than 90 seconds (either via water pump directing seawater into its mouth or through full submersion within a transportation enclosure). Just prior to release, all sunfish should be marked, either with visual ID tags or electronic transmitters (i.e., satellite or acoustic). Indeed, best practices for attaching pop-off archival satellite tags were determined through aquarium and research scientist collaboration in the late 1990s using captive specimens and subsequently used for sunfish tagging studies (e.g., Dewar et al. 2010, Thys et al. 2015; Fig. 10).

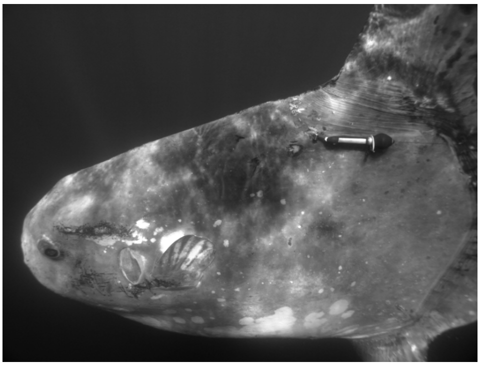

Figure 10. Ocean sunfish with pop off archival tag inserted at the base of the dorsal fin. Photo taken and permission granted by: Wyatt Patry.

Remaining Questions

Significant advances in husbandry techniques over the past several decades have made it easier to exhibit and rear ocean sunfishes. As with any discipline, there is scope for continual refinement. As field studies provide further insights into the biology of sunfishes, information on dietary composition and shifts, biomechanics and morphometrics will all help towards this goal. However, further information is required on the bioenergetics of sunfish so that scaling factors such as metabolic rate and cost of transport can be balanced against daily caloric intake. A deeper understanding of the high parasitic burden that characterize many wild sunfishes (Ahuir-Baraja 2020 [Chapter 10]) may help with the development of targeted medical procedures, and improved protocols during the early stages of transportation and quarantine.

The reciprocal is also true with information from sunfish in aquariums helping to address otherwise intractable questions arising from the field. For example, understanding the rate at which particular prey items are assimilated into different body tissues, or mucus is a fundamental challenge when seeking to reconstruct diets using biochemical approaches such as stable isotopes (Phillips et al. 2020). Under captive conditions, using isotopically labelled foods, such challenges could be overcome. Likewise, the reconciliation of electronic traces from multi-channel data loggers (e.g., tri-axial accelerometers) against known behaviors could be conducted in large display tanks with minimal stress to the study animal, collected mucus and blood samples can also provide information on nutritional status, immunological responses to stress or injury and the level of stress conditions through the presence of certain hormones (study in progress, Monterey Bay Aquarium). Maturity status may also be determined through the presence and quantities of sexual hormones (Du et al. 2017). In addition, if ultrasonography or X-ray radiography could be performed, it may be possible to determine non-invasively, not only visceral diseases but also gender by visualizing gonad appearance and shape (Martin-Robichaud and Rommens 2001, Colombo et al. 2004). Continuing in this vein, captive reproduction and larval culture of the ocean sunfish is another potentially rich research avenue. Knowledge of sunfish reproduction is limited (although see Forsgren et al. 2020 [Chapter 6]), and to date there are no known records of observed courtship rituals nor spawning in either aquarium or natural settings. Public aquariums increasingly have the ability to house multiple mature specimens. The concepts of providing suitable habitat for courtship and spawning (including seasonal adjustments to photoperiod and temperature) along with a means to collect fertilized eggs are well ingrained into the missions of public aquariums. It may be only a matter of time until the opportunity to culture larval ocean sunfish becomes a reality. Lastly, it is evident that field biologists benefit greatly from sunfish on display by boosting public interest and political awareness of this often-overlooked species.

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CHAPTER 15

Unresolved Questions About Ocean Sunfishes, Molidae

A Family Comprising Some of the World's Largest Teleosts

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Introduction

The ocean sunfishes, family Molidae, currently consist of five species classified in three genera, including the largest of the teleostean fish, *Mola alexandrini* (Sawai et al. 2018), which can exceed 2,300 kg (see Sawai et al. 2020 [Chapter 2] and Caldera et al. 2020 [Chapter 3]). The other four species

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[#] For affiliations see end of the chapter

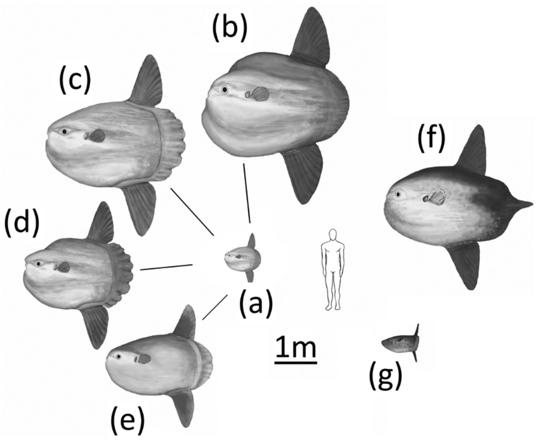


Figure 1. Key questions remain around the taxonomy of ocean sunfishes. Currently five species are recognized. a. Juvenile *Mola* spp., b. *Mola alexandrini*, c. *Mola mola* v1, d. *Mola mola* v2, e. *Mola tecta*, f. *Masturus lanceolatus* and g. *Ranzania laevis*. *M. mola* can have a variety of morphologies ranging from those with a head bump and wavy clavus to those with no head bump and a less slightly scalloped clavus. These different morphologies occur in both Atlantic and Pacific basins and can become more pronounced when individuals are in captivity. (See Caldera et al. 2020 [Chapter 3] for more details.) At small sizes, *Mola* spp. as seen in (a) *M. alexandrini* (b) *M. mola* (c,d) and *M. tecta* (e) are difficult to distinguish from each other. Illustration credit: Jamie Watts.

include *Mola mola*, *Mola tecta*, *Masturus lanceolatus* and *Ranzania laevis* (Fig. 1). As with studies of other marine megafauna, it is an exciting time for ocean sunfish research. Growing interest in the group, combined with emerging techniques, is driving new discoveries. For example, satellite tags have revealed the use of ocean depths to beyond 1000 m (Thys et al. 2017), animal-borne cameras and metabarcoding analyses are shedding light on diet and feeding behaviors (Nakamura et al. 2015, Sousa et al. 2016a), while genetic and morphological research have helped reveal the first new *Mola* species to be identified in 125 years (Nyegaard et al. 2017). However, many ocean sunfish mysteries still remain. For example, total fecundity remains unknown for any molid species despite Schmidt's (1921) often cited report (based on a single specimen) that *Mola mola* is the most fecund vertebrate on earth. It is therefore timely to take stock of our current knowledge of ocean sunfishes and triage important areas for future research. Following the theme of expert identification of key scientific research questions (e.g., Hays et al. 2016), we here synthesize recent findings, identify knowledge gaps and suggest tactics and techniques for rapidly advancing the field of ocean sunfish research.

Methods

Experts in the field of ocean sunfish biology were invited to contribute chapters to a book on ocean sunfishes (The Ocean Sunfishes: Evolution, Biology and Conservation) summarizing their fields of expertise and identifying remaining knowledge gaps. Key questions are summarized here along with potential methods and collaborations that could help advance the search for answers.

Results and Discussion

Diets of Ocean Sunfishes

The historic view that ocean sunfishes are obligatory jelly eaters has at last been overturned with the recent confirmation that *M. mola* diets change with age, shifting from benthic foraging to more pelagic prey as individuals grow larger (Phillips et al. 2020 [Chapter 9]). This realization is not new, as Fraser-Brunner (1951) reported that sunfish boast a diverse diet of fishes, squids and crustaceans as well as jellies. However, it took recent studies in the Mediterranean, NW Pacific (Japan) and NE Atlantic (Portugal) to finally consolidate our view that small molid individuals tend to occupy coastal areas and feed broadly on neritic invertebrates and fish, while larger specimens appear to live predominantly in the open ocean and have diets focused more on gelatinous zooplankton (Harrod et al. 2013, Nakamura and Sato 2014, Sousa et al. 2016a, Syväranta et al. 2012, Phillips et al. 2020). More studies of this type are needed to assess if size-related changes in habitat and diet occur more broadly across geographical areas and across all molid species. Here a range of techniques may help address questions of diet, including direct observations from animal-borne cameras (Nakamura et al. 2015), metabarcoding analysis of gut content or fecal samples (Sousa et al. 2016a), as well as stable isotope analysis (Syvaranta et al. 2012, Harrod et al. 2013, Nakamura and Sato 2014, Phillips et al. 2020).

For the latter, the use of compound specific stable isotopes (Phillips et al. 2020) warrants further attention given that this method, although considerably more expensive than bulk isotopes, can overcome issues with identifying correct nitrogen baselines for broad-ranging fishes (which vary markedly in space and time). Such research could reveal what drivers underlie ontogenetic dietary and habitat shifts including (i) the loss of agility in larger individuals to target small benthic or more maneuverable prey, (ii) biomechanic costs of transport linked to large body size, (iii) rapid growth and large size to reduce the pool of predators, and (iv) changing nutritional needs with body size.

Diet studies also need to consider the foraging ecology of sunfishes in the open ocean in addition to nearshore waters, where most research has focused (Fig. 2a). While information about the ecology

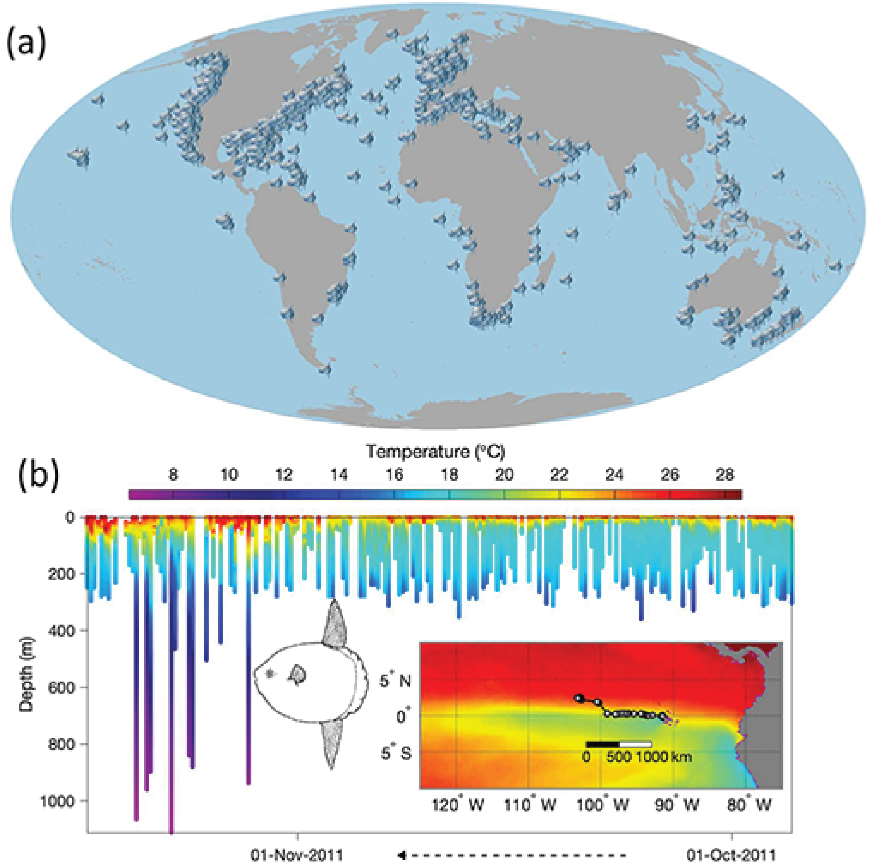


Figure 2. Ocean sunfish sightings and diving behavior. (a) Crowd-sourced sightings records for ocean sunfishes (www.oceansunfish.org) tend to be biased to near-shore areas where observer effort is greater. (b) Dive profile of a *M. alexandrini* tracked in the equatorial Pacific (modified with permission from Thys et al. 2017).

of ocean sunfishes in open-ocean areas is lacking, this may be a key habitat. Biologging studies and direct observation from submersibles have shown that sunfishes can on occasion dive deeper than 1000 m (Fig. 2b) and can spend long periods at 200–300 m (Sims et al. 2009a, Phillips et al. 2015, Thys et al. 2017), although their behavior at these depths is still poorly understood. One possibility is that sunfishes are feeding at depth on colonial gelatinous zooplankton such as siphonophores, salps and pyrosomes (Potter and Howell 2011, Nakamura et al. 2015, Phillips et al. 2020) or perhaps large deep-sea medusae such as *Stygiomedusa gigantea* (Benfield and Graham 2010). Interestingly, tracking data show that when in oceanic regions, their range of depths occupied is broadly similar to adult leatherback turtles that feed primarily on gelatinous zooplankton (Houghton et al. 2008).

In line with observations by Sims et al. (2009a), Nakamura et al. (2015) postulated that sunfishes may also feed upon bioluminescent prey given the evidence of their extensive nighttime excursions below 50 m. Similar strategies have been suggested for other gelativores (e.g., leatherback turtles, Davenport and Balazs 1991), but empirical data of sunfish feeding at depth are currently lacking. In the future, animal-borne cameras and other biologging techniques may resolve their feeding ecology below 200 m (Nakamura et al. 2015). Investigating the expression of visual opsin genes for both rod and cone photopigments could also help determine to which colors sunfishes are most attuned and if they have the visual sensitivity to see and target bioluminescent prey (Musilova et al. 2019). Such inquiry into sunfish visual acuity at low light levels will add insight into their prey foraging capacities during descent, ascent (e.g., silhouette hunting) and various phases of their deep dives.

Foraging Physiology and Ecology

We should also consider the biochemical composition of prey and how it relates to sunfish physiology (Hays et al. 2018). For example, gelatinous zooplankton may be rich in collagen (e.g., some species boast 69 percent collagen by dry mass; Khong et al. 2016), which may be important for the development of the thick subcutaneous layer known as the hypodermis (Davenport et al. 2018, Watanabe and Davenport 2020 [Chapter 5], Bemis et al. 2020 [Chapter 4]). The hypodermis has been suggested to play a central role in buoyancy (Arakawa and Masuda 1961, Watanabe and Sato 2008, Davenport et al. 2018), but it may be equally important in retaining heat through thermal inertia during deep and/or cold water feeding. Certainly, sunfishes appear to display a passive thermoregulatory strategy, which seems to reflect the physiological attributes associated with a large body mass, rather than physiological mechanisms. Specifically, larger sunfishes have lower heat-transfer coefficients, suggesting they also benefit from their large body masses to keep their body warm during foraging dives to deep, cold waters (Nakamura and Sato 2014).

Advances in understanding the foraging ecology of sunfish requires integration of animal tracking, environmental sensing, and ecosystem sampling. Satellite remote sensing is essential because of the large spatial scales over which sunfish migrate. Sunfish migratory paths have been associated with large scale open-ocean features such as the Pacific equatorial upwelling front (Figure 2b; Thys et al. 2017), as well as smaller scale, more ephemeral fronts in coastal upwelling habitat (Thys et al. 2015). While studies of sunfish migration patterns have effectively used relatively low accuracy (~ 100 km) position data from tags (Sousa et al. 2020 [Chapter 8]), understanding foraging ecology requires high accuracy tracking, particularly in ocean margin ecosystems having strong environmental gradients. In these systems high accuracy tracking provides certainty in defining relationships between sunfish and oceanographic features. For example, in the southern California Current System, GPS tracking of a sunfish and satellite sea surface temperature data revealed consistent habitat occupancy in coastal upwelling fronts throughout an 800 km migration, synthetic aperture radar images indicated convergent circulation in these fronts, and *in situ* net tow data revealed maximum concentrations of gelatinous prey at the warm side of these fronts (Thys et al. 2015). Improved information on the movements of sunfish will help identify key areas for targeted conservation, which has been an important goal in tracking studies with other marine megafauna (Hays et al. 2019, Queiroz et al. 2019).

Bioenergetics and Fasting Endurance

There is a need to develop robust bioenergetic models that explain how metabolic demands are met by feeding on different prey groups, particularly as body size increases. We need to better understand both the energetic content of different prey items and whether the energy density of different parts of prey is linked to selective feeding. For example, some low energy-density prey, such as scyphozoan jellyfish, may have body components (e.g., gonads) that are relatively energy rich (Doyle et al. 2007, Lucas et al. 2011) and therefore may be targeted by predators (Lucas et al. 2011, Hays et al. 2018). Techniques, such as the use of animal-borne cameras (Nakamura et al. 2015) and direct observations have started to reveal how some marine predators, e.g., penguins (Thiebot et al. 2017) can feed selectively on high energy density parts of prey (Milisenda et al. 2014, Nakamura et al. 2015). The use of this sort of technology is still in its infancy with ocean sunfishes, but shows great promise.

Bioenergetic models tend to focus on feeding rates and assimilation efficiency (i.e., energy intake) versus metabolic rate (Lawson et al. 2019). However, it is now well known that prey fields for ocean predators are not homogenous but rather prey is often patchily distributed. Consequently, there may be long intervals between encounters with rich prey patches (Sims et al. 2009b). With this in mind, it is important to understand how prey encounter rates relate to fasting endurance, for this relationship may be a key aspect of the foraging ecology of wide-ranging ocean predators (Hays et al. 2018). These links have been reported infrequently for ocean sunfishes, with the notable exception of Nakamura et al. (2015) who combined multichannel data loggers and HD cameras to determine prey selectivity and encounter rates for ocean sunfish (See Figure 6 in Nakamura et al. 2015).

We can also learn from developments in the ecology of taxa feeding on gelatinous zooplankton. For example, Thiebot et al. (2017) using similar technology to Nakamura et al. (2015), revealed that four species of penguins routinely feed on pelagic gelatinous organisms (gelata), and provided invaluable data on search time and encounter rates. Such empirical foraging data (encompassing prey encounter rate, selection, consumption, and handling time) can open the door to field-based studies of optimal foraging via functional response (e.g., Hays et al. 2018). This approach would drive a step change in our capacity to construct bioenergetics models. Likewise, movement data from leatherback turtles (*Dermochelys coriacea*) tracked for up to one year suggest individuals feed in jelly blooms only for about 30 percent of their time (Bailey et al. 2012). Thus, long fasting endurance may be the key requirement for a predator to feed only on jellies, with adult leatherback sea turtles likely having a particularly long fasting endurance of more than six months (Hays and Scott 2013).

One consequence of an ontogenetic shift from a broad diet to a more gelatinous zooplankton diet, is that prey may become increasingly patchily distributed (Houghton et al. 2006). From a theoretical viewpoint, fasting endurance is theorized to increase with body size, since metabolic rate typically scales with an exponent of less than one, while body reserves scale with an exponent close to one. In other words, as animals get larger, their mass-specific metabolic rate decreases, but their mass-specific energy stores stay broadly the same (Lindstedt and Boyce 1985). Work in this area has tended to focus on mammals, with the conclusion that the fasting endurance (i.e., the ratio of energy reserves to metabolic rate) increases in larger individuals (Lindstedt and Boyce 1985). However, the same key drivers likely hold true for fish. Typically metabolic rate is reported as $R = aM^b$, where R = metabolic rate and M = body mass. A great range of scaling exponents (b in the equation) have been reported across different fish species. For example, Killen et al. (2010) reported a mean scaling exponent of 0.698 for open-water pelagic fish, 0.776 for bentho-pelagic fish and 0.802 for benthic fish. This range of exponents across species broadly reflects that reported in other studies (e.g., Lawson et al. 2019) and means that larger fish will have a lower mass-specific metabolic rate. For example, using an exponent of 0.698, the mass-specific metabolic rate of a 1000 kg fish is predicted to be 20 percent of the metabolic rate of a 5 kg fish. Thus, we might expect that larger ocean sunfishes will have a longer fasting endurance than smaller individuals (Fig. 3). An increase in fasting endurance with body size may be key to the survival of large sunfishes feeding on gelatinous plankton, with individuals being able to survive long periods between encounters with rich prey patches. However,

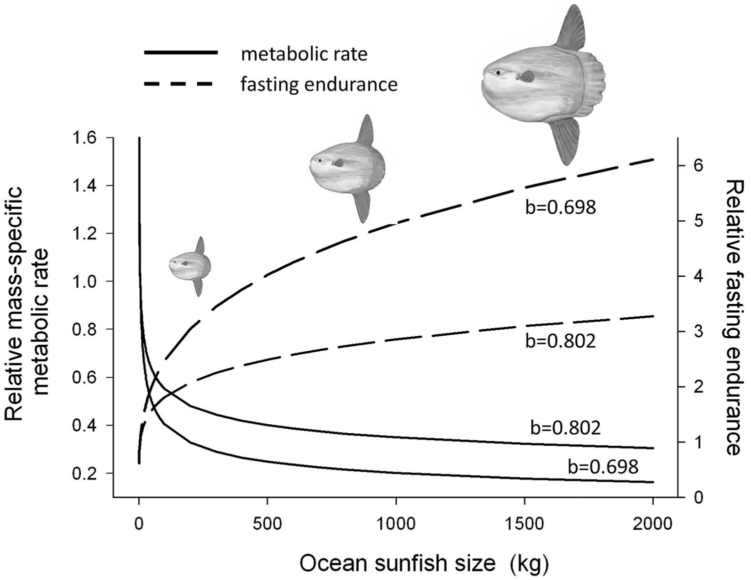


Figure 3. Is fasting endurance the key to a diet of patchily distributed gelatinous plankton? The mass-specific metabolic rate tends to decrease with animal size and hence fasting endurance increases. Typically metabolic rate is reported as $R = aM^b$, where R = metabolic rate and M = body mass. Solid lines represent the estimated mass-specific metabolic rates of different sized ocean sunfish (*Mola mola*) using two different scaling exponents between body size and metabolic rate (0.698 and 0.802), reflecting the range reported by Killen et al. (2010). Dashed lines represent the relative fasting endurance of different sized sunfish, which are derived from the mass-specific metabolic rates (assuming mass-specific energy reserves scale with body size to the power one). Values are expressed as a proportion of the values for a 5 kg fish. The plots show that fasting endurance likely increases in larger ocean sunfish. Improving estimates of this relationship requires data on the metabolic rate of ocean sunfish across a broad range of body sizes. Sunfish images credit: Jamie Watts.

aside from these general predictions based on metabolic rate measurements for other fish species, there remain key unresolved questions regarding the metabolic rate, energy stores and fasting endurance of different sized sunfishes.

Innovative biologging techniques that can record individual prey capture events may resolve how periods of feeding versus fasting change with body size in sunfishes. Furthermore, movement trajectories from tracking may reveal periods of feeding versus transit legs between prey patches (e.g., Sims et al. 2009b) as have been achieved for pelagic sea turtles. In time, measuring metabolic rates for ocean sunfishes (scaled for body mass and activity level) may become feasible. Although seemingly intractable for such large fishes (excluding *Ranzania* sp.), the recent development of the *in situ* mega-flume allowed Payne et al. (2015) to gather swimming metabolic rates for a 2.1 m, 36 kg zebra shark (*Stegostoma fasciatum*) under natural conditions. Similar data would help us refine scaled estimates of cost of travel (required in bioenergetic models) and complement recent advances in our understanding of sunfish biomechanics and locomotion (Watanabe and Sato 2008, Davenport et al. 2018).

Biomechanics and Breaching

A better understanding of how swimming behavior relates to foraging ecology of different sizes and species of wild ocean sunfishes (Sousa et al. 2020 [Chapter 8], Phillips et al. 2020 [Chapter 9]) is also needed. Studying the biomechanics of fast locomotion (i.e., sprints) in ocean sunfish may hold clues to various aspects of foraging and predator avoidance (*sensu* Soto et al. 2008, Wilson et al. 2018). Sunfishes under 2 m are also known to breach, with repeated reports of this behavior being made off California (see Fig. 2A in T. Thys et al. 2020 [Chapter 14]), New England (C. Carson personal observation), Italy (N. Phillips personal observation), Bali (Konow et al. 2006) and Angola (C. Weir personal observation). Various explanations for the adaptive significance of breaching have been put forth including dislodging ectoparasites, ditching overly zealous cleaner fishes (Konow et al. 2006), or avoiding predators. All, however, warrant formal testing.

Also of note are the major ontogenetic changes that occur in molid morphology including the shape, size and angle of their dorsal and anal fins and disproportionate thickening of their hypodermis (Watanabe and Davenport 2020 [Chapter 5]). How these dramatic morphological changes impact swimming ability and movement patterns, can be addressed through the use of animal-borne biologging with accelerometers, cameras and depth sensors.

Anatomy, Taxonomy and Evolution

Many questions remain with regards to molid anatomy, including the strange nature of their bones, which are spongy, fibrous and easily sliced with a knife. The unique gills, circulatory patterns, and large hearts of molids likely hold more clues to the group's evolutionary success and to their physiological abilities for diving. However, few specimens are properly preserved and available for study in natural history museums. In most cases, we simply lack sufficient specimens to study these organ systems in very large individuals (> 2.5 m, Bemis et al. 2020 [Chapter 4]). Also important is the need for well-fixed larvae and juvenile specimens for future histological study of anatomical systems including the nervous system, swim bladder and sensory organs.

Key questions in molid phylogenetic studies involve the number of valid, extant species of ocean sunfishes (Fig. 1). For example, are there different species of *Mola mola* in different ocean basins (Sawai et al. 2020 [Chapter 2])? Is the current monotypic status of the *Ranzania* and *Masturus* genera valid? More detailed information on morphological changes with growth across different species is crucial to establish unambiguous identification keys. Currently, there is no way to identify, from morphology alone, small individuals in the genus *Mola* to species. There is also considerable variation in the head, snout and chin bump features of *Mola* spp. that often, but not always, varies with size (Sawaii et al. 2020 [Chapter 2], Caldera et al. 2020 [Chapter 3]). Morphologic and genetic analyses of individuals possessing these possibly hybrid traits will be informative and essential to understanding the taxonomy of the group as a whole.

With only a fragmentary fossil record, the evolutionary history of ocean sunfishes remains poorly resolved as well. For example, most of the pre-Miocene history (> 23 million years ago) of ocean sunfishes is completely unknown, while the anatomy of now extinct species (*Mola pileata* and *Ranzania* spp.) that were relatively common in the Miocene (23 to 5 million years ago) is known only from isolated beaks and dermal plates (Carnevale et al. 2020 [Chapter 1]). Future fossil finds, particularly in the Oligocene (34 to 23 million years ago), will further illuminate the hidden pathway to modern molids.

Population Structure, Genetic Identity, eDNA and Trait Derivation

A host of questions remain concerning molid species' identity, population structure and size. To date, everything we have learned regarding phylogenetics and population genetics of molids has been based on Sanger sequencing of mitochondrial genes (reviewed in Caldera et al. 2020 [Chapter 3]). Remaining questions can now be addressed with emerging techniques benefiting from advances in next-generation sequencing technologies including genome-wide SNP (single nucleotide polymorphism) genotyping (e.g., RADseq). Environmental DNA (commonly referred to as eDNA), can also be used to assess the occurrence and seasonality of molids from seawater samples, as is already conducted for other fish taxa (e.g., sharks in Truelove et al. 2019). Genetic approaches can address fundamental questions including: (i) how many molid species exist, what are their geographic ranges, and do they hybridize? (ii) how and when did different molid species and populations emerge (e.g., molecular clock studies)?

(iii) how genetically connected are populations in different ocean basins? and (iv) what are the genetic underpinnings of their specialized traits like the reduced skeleton and thick hypodermis?

Growth Rates, Ageing and Reproductive Biology

While growth rates of ocean sunfishes in captivity are widely measured to help assess animal health and well-being, rates for free-living individuals are unknown. It is likely that captive molas receive much larger and more calorie-rich rations than wild molas, so growth rates may be artificially high in captivity. Key questions surrounding the links between diet, environmental conditions and growth remain poorly resolved. To improve long-term aquarium rearing conditions and husbandry management, wild growth rates are much needed. In addition, acquiring baseline data on the condition and histological status of internal organs for wild specimens would provide invaluable benchmark information for aquarists to assess organ condition and function over time for captive specimens (Howard et al. 2020 [Chapter 13]). Since it is unknown whether sunfishes are sexually dimorphic, developing blood assays or other methods to assess sex and level of maturity in sunfishes would also offer interesting insight.

Another major gap in our knowledge of sunfishes involves measuring their lifespan in the wild. Ageing sunfishes remains a challenge. Their strange ear bones (i.e., otoliths and octoconia; Nolf and Tyler 2006), are composed of vaterite rather than the more typical teleost aragonite (Gauldie 1990) and are not easily aged. Additional techniques such as measuring central corneal thickness and/or using radiocarbon dating to measure the carbon isotopes in their eyes, as done in Greenland sharks (Nielsen et al. 2016) may hold promise and are worthy of investigation.

Knowledge of the reproductive biology of sunfishes also remains limited (Forsgren et al. 2020 [Chapter 6]), with no observations of spawning in nature or captivity. Few large animals have been examined and total fecundity remains unknown for any molid species. For free-living individuals, spawning aggregations might be uncovered through citizen science or animal-borne cameras which could also help aquariums create suitable conditions for spawning. Likewise, drones are now widely used across other taxa to help assess abundance and interactions (Schofield et al. 2019) and may have merit in locating and assessing potential molid spawning aggregations. Long-term tracking of multiple mature individuals might also reveal spawning areas (Thys et al. 2020 [Chapter 7]), but further information on size at maturity (Nakatsubo et al. 2008, Forsgren et al. 2020 [Chapter 6]) is required from different sites.

Effects of Parasites on Sunfish Behavior and Overall Welfare

Understanding the pathological and ecological host consequences of infection is the next major goal for sunfish parasitology (Ahuir-Baraja 2020 [Chapter 10]). Specifically, an understanding of how parasite attachment locations and feeding modes affect growth, locomotion, buoyancy and survivorship is needed. Observational studies at cleaning stations are also recommended, given that individual sunfish allocate significant time to this behavior (Konow et al. 2006, Thys et al. 2017), which suggests parasites could be a major stressor. Where parasites are thought to be ingested together with prey, there is scope for collaboration with trophic ecologists to quantify at what size sunfish start to feed upon particular prey items. Where prey is spatially defined, it may also be possible to use parasites as indicators of broad-scale movements, either horizontally or throughout the water column. This logic extends to the use of parasites as biological tags, an approach that has been used with great success in other wide-ranging fishes (Marcogliese and Jacobson 2015). Furthermore, comparative studies of parasitic species abundance and diversity in juvenile and adult molids may shed more light on ontogenetic shifts in sunfish diet (e.g., Nakamura and Sato 2014, Sousa et al. 2016a, Phillips et al. 2020, Phillips et al. 2020 [Chapter 9]). It is also noteworthy that juvenile sunfish swim in schools (Abe et al. 2012) which may influence transmission of ectoparasites during early life history stages.

Established protocols for the collection of parasite data in areas of high bycatch need to be developed and disseminated widely so that such information becomes interwoven more routinely into overall studies of sunfish ecology. In turn, these data can help aquarists in refining their husbandry practice.

Elemental Pollution

While a baseline examination of trace element dynamics has been conducted mainly in Atlantic ocean sunfish populations (Baptista et al. 2020 [Chapter 11]) understanding bioaccumulation effects of these elements is unknown. Some elements are known to disrupt fish physiology, reproductive success and increase fish mortality at certain levels (Dunier 1996, Authman et al. 2015). Further ecotoxicological studies could explore physiological effects using a variety of elemental treatments administered in a controlled setting on small captive sunfish (or perhaps even their more accessible phylogenetic relatives such as pufferfish) (e.g., Holdway and Sprague 1979, Lushchak et al. 2009, Ricketts et al. 2015, Wang et al. 2016). Alternatively, measuring elemental concentrations and conducting histology studies of gill and liver tissues where deformities due to elemental accumulation can occur (Gaber 2007) may provide added insight into the threshold level at which elements impact fish physiology.

Plastic Pollution

The impacts of plastic debris, from micro (≤ 5 mm) to meso (5–25 mm) to macro (> 25 mm), are pervasive concerns across all marine taxa, yet little is known about these impacts on ocean sunfishes. *Mola* have been known to ingest plastics as a result of eating monofilament attached to baited hooks and through ingested microfibers (Baptista et al. 2020 [Chapter 11]) wherein 80 percent of the individuals examined had at least one microfiber in their guts. The impact of these ubiquitous contaminants however is largely unknown and deserving of more attention.

Climate Change, Horizontal and Vertical Range Shifts

Many marine taxa (reviewed in Edwards 2016) are experiencing changes in their phenology, abundance and distribution due to climate change (Pinsky et al. 2013, Poloczanska et al. 2013, Halpern et al. 2019), yet how these influences affect sunfishes remain unclear. It is well documented that isotherms (lines of equal temperature) are generally moving polewards at a rate of > 100 km per decade in some places (e.g., McMahon and Hays 2006). Tracking studies have identified seasonal poleward movements of ocean sunfishes in the north Pacific (Dewar et al. 2010) and northeast Atlantic (Sims et al. 2009a, Sousa et al. 2016b). A shifting position of the summer isotherms will likely influence the extent of poleward migration of sunfishes. Changes in the trailing edge of animals distributions can be faster than the poleward edges (Robinson et al. 2015) so tracking studies of molids should also pay attention to possible loss of more equatorial habitats. The horizontal range of ocean sunfishes may be changing accordingly, a suggestion further supported by increased sightings in the northern latitudes of Iceland (Palsson and Astthorsson 2017) and Norway (Frafjord et al. 2017). Whether or not sunfishes are adjusting their vertical behaviors and shifting their preferred cleaning stations to be in deeper water based on ocean warming also remains a question. Further tracking studies, at-sea surveys of distribution (Breen et al. 2017) and *in situ* observations at cleaning stations, particularly in the mesophotic zones, will help clarify the extent of these range changes (Sousa et al. 2020 [Chapter 8]).

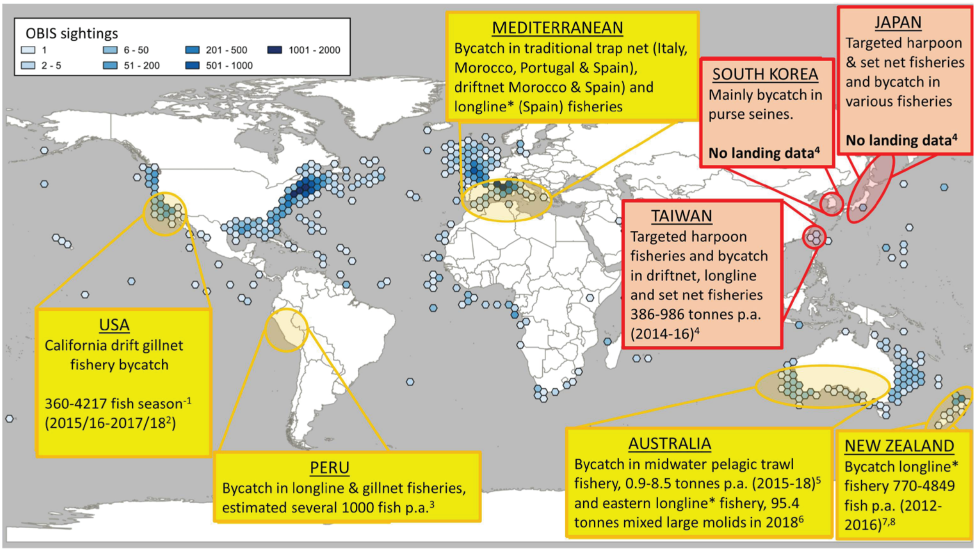
Crowd-Based Science, Non-Invasive Tracking, Skin and Color patterns

Harnessing and honing the power of crowd-based sunfish sightings (for example, www.oceansunfish.org, New England Coastal Wildlife Alliance (NECWA) tracking form at www.nebshark.org, molaphotos@outlook.com, MatchMyMola at (http://www.thebalisunfish.org/matchmymola/) offer a powerful means of collecting tissue samples for a wide array of studies including stable isotope and genetic analyses. These datasets can also offer a means of potentially tracking sunfish non-invasively. With their plethora of skin patterns and scarring, individual sunfish can theoretically be tracked visually given sufficient representative photographic material that can be supplied by SCUBA divers or ecotourism groups. The presence of sunfish on social media and the internet (Thys et al. 2020 [Chapter 14]) coupled with image recognition software and machine learning may help to improve both the quantity and quality of crowd-sourced observations, and make these datasets increasingly more valuable. Additional uses of well-curated crowd-sourced visual databases could be to: assess the variability of sunfish skin and color patterns during different behaviors, times of day and seasons; ascertain whether skin and color patterns are stable over time and; establish the basis for assessments of injury types and frequency.

Crowd-based sightings and reports can also reveal mass strandings and die-off events of *Mola mola* as witnessed between September and December 2019 on both the east (C. Carson personal communication) and west coast of the USA (T. Thys unpublished data). These observations can be coupled with environmental data to glean a better understanding of the factors underlying past stranding events noted for *M. mola* in Monterey Bay (Gotshall 1961) and for *Ranzania laevis* in Western Australia (Smith et al. 2010) and South Africa (L. Nupen personal communication).

Bycatch, Targeted Fisheries and Population Trends

Threats to ocean sunfishes are poorly documented although it is known that large numbers are caught as bycatch in commercial fisheries (Nyegaard et al. 2020 [Chapter 12]). While individuals accidentally caught may be released alive (Phillips et al. 2020 [Chapter 9]), post-release survival is unknown. For example, in the Moroccan driftnet fishery, the estimated bycatch was 36,450 in one year (Pope et al. 2010). Yet beyond these incidental 'hotspots' (Fig. 4), information on bycatch for all molid species is



MEDITERRANEAN
Bycatch in traditional trap net (Italy, Morocco, Portugal & Spain), driftnet Morocco & Spain) and longline* (Spain) fisheries

SOUTH KOREA
Mainly bycatch in purse seines.
No landing data[4]

JAPAN
Targeted harpoon & set net fisheries and bycatch in various fisheries
No landing data[4]

TAIWAN
Targeted harpoon fisheries and bycatch in driftnet, longline and set net fisheries 386-986 tonnes p.a. (2014-16)[4]

USA
California drift gillnet fishery bycatch
360-4217 fish season^{-1} (2015/16-2017/18[2])

PERU
Bycatch in longline & gillnet fisheries, estimated several 1000 fish p.a.[3]

AUSTRALIA
Bycatch in midwater pelagic trawl fishery, 0.9-8.5 tonnes p.a. (2015-18)[5] and eastern longline* fishery, 95.4 tonnes mixed large molids in 2018[6]

NEW ZEALAND
Bycatch longline* fishery 770-4849 fish p.a. (2012-2016)[7,8]

Figure 4. Ocean sunfish face fishing pressure across their broad range. World map showing locations of sightings for combined genera *Mola* and *Masturus* drawn from OBIS data (www.obis.org) accessed 10/1/2020 (total records 19,353). Commercial fisheries landing large molids are highlighted in red, those known to experience considerable levels of large molid bycatch are highlighted in gold. 1 Mason et al. (2019). 2 Common mola seasonal (1 May to 31 January) bycatch in the California drift gillnet swordfish fishery estimated from NOAA (2019): proportion of sunfish in observed nets and the number of total nets set. 3 Mangel et al. (2019). 4 FAO (2018). 5 AFMA (2019a). 6 AMFA (2019b). 7 MPI (2016). 8 MPI (2017).
* Large molids are widely reported as bycatch in pelagic longline fisheries worldwide but accurate estimates are not currently possible for most fisheries (see main text).

either lacking or sporadic, requiring further investigation and collation. Whether sunfish are captured via directed take or bycatch, the implications of removing large numbers of individuals from any system requires further attention. As we have moved beyond the notion of sunfishes being life-long gelatinous animal specialists, these implications will change in line with the size of individuals taken, and the complexity of the community from which they were removed. With some certainty we can say that large aggregations of small sunfish found in temperate and subtropical coastal seas exert a degree of top down control on both pelagic and benthic food webs (Grémillet et al. 2017), at least on a seasonal basis. Thus, their removal may have multi-faceted and profound effects.

More strikingly, we have yet to understand the connectivity and shared genetic heritage of seemingly independent aggregations of sunfish, whereby the extirpation from one region may have wide ranging ramifications for other sites. Filling these knowledge gaps will require a combination of trophic, molecular and tracking studies.

Additionally, we have a poor understanding of overall trends in abundance and effective populations sizes of any sunfish species. In the context of bycatch and emergent fisheries, such data are vital (Liu et al. 2015, Nyegaard et al. 2020 [Chapter 12]), especially where policy recommendations hinge on information relating to favorable conservation status. Again, a combination of approaches will be required starting with mark-recapture studies to assess whether areas of high bycatch are simply recapturing the same individuals. There is also an opportunity here to work with fisheries to gather much needed life history information from caught specimens including data on gonad maturity stage for assessing reproductive status and fecundity.

Concluding Remarks

We hope that this compilation of key questions for ocean sunfish research helps to convey the growing interest in and knowledge of the biology of this fascinating group of fishes. Emergent techniques will certainly help drive ocean sunfish research forward, and transform our capacity to study individuals under natural conditions. At the same time, work with other marine megafauna has revealed the huge value of collaborations across disciplines, with for example, the collaborative work of ecologists, mathematicians, physicists, oceanographers, engineers, and information technologists being used to identify general patterns in animal movement (e.g., Sims et al. 2008, Humphries et al. 2010, Harcourt et al. 2019). Such collaboration may open up new directions for ocean sunfish research. Future work also needs to consider ethical concerns of some techniques, such as long-term deployment of satellite tags, where continued refinement of tag design and attachment techniques can help minimize impacts to the fish. We hope that this horizon-scanning exercise will help promote work on ocean sunfishes.

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