Ocean sunfish, genus *Mola* Kölreuter, 1766 (Pisces Molidae), exhibit surprising levels of agility during interactions with orca, *Orcinus orca* (Linnaeus, 1758) (Mammalia Delphinidae)

Marianne Nyegaard*1,2, Ingrid N. Visser3 & London A. Fletcher3,4

ABSTRACT

Ocean sunfish (*Mola* spp.) are well known for their large adult size and peculiar morphology, which in combination give them the resemblance of a giant, swimming fish head. At first glance, this unusual body form hints at locomotive ineptitude, and traditionally molids have indeed been considered poor swimmers. Although this archaic view has been thoroughly rebutted in recent years, with studies revealing molids are strong swimmers (for example their ability to rapidly accelerate, with recorded burst speeds for *Mola mola* of 6.6 m/s), their fine-scale maneuverability is unclear. Furthermore, many natural molid behaviours are not well understood, including antipredator behaviours, as opportunities to observe this taxa in the wild are limited. Unexpectedly, during a recent global review of molid interactions with orca (a molid predator), a number of video recordings revealed surprisingly rapid and agile molid movements. These included the molids turning up-side down, rolling backwards, pivoting and spinning. These behaviours appeared to be deliberate attempts on behalf of the molids to keep the clavus ('tail') towards the orca, keep the ventral area away, evade the orca, and/or discourage the orca from making physical contact. Here, we describe eight 'Evade' behaviours based on video analysis, present detailed descriptions and provide examples.

KEY WORDS

Molid; killer whale; evasive behaviour; anti-predator behaviour; predator-prey interaction.

Received 28.09.2022; accepted 02.12.2022; published online 16.02.2023

INTRODUCTION

Molid species from the genus *Mola* (Family Molidae) are large marine, epipelagic - mesopelagic fishes, ubiquitous to tropical and temperate waters. Currently, three species are recognised; the ocean sunfish *Mola mola* (Linnaeus,

1758), giant sunfish *Mola alexandrini* (Ranzani, 1839) and hoodwinker sunfish *Mola tecta* Nyegaard et al., 2017 (Fricke et al., 2022; Sawai et al., 2018) (although we note not all agree on the nomenclature; Britz, 2022), hereafter referred to as molids. At least one species, *M. alexandrini*, can attain over 3.3 m in total length (TL) and over 2.7

¹Ocean Sunfish Research Trust, Auckland, New Zealand - https://orcid.org/0000-0002-9920-2862

²Auckland War Memorial Museum Tamaki Paenga Hira, Natural Sciences, The Domain, Private Bag 92018, Victoria Street West, Auckland 1142, New Zealand

³info@orcaresearch.org, Orca Research Trust, P.O. Box 402043, Tutukaka, 0153, New Zealand - https://orcid.org/0000-0001-8613-6598

⁴Aquatic Research Conservancy, Blaine, Washington State, USA - https://orcid.org/0000-0002-8078-4962

^{*}Corresponding author, e-mail: mnyegaard@oceansunfishresearch.org

tons in body weight (Gomes-Pereira et al., 2022), heavier than any other extant bony fish species (Sawai & Nyegaard, 2022). Molids are notable for their unusual morphology, whereby instead of a tail, elements from the dorsal and anal fins form a rudder-like back-end, termed a 'clavus' (Fraser-Brunner, 1951; Johnson & Britz, 2005). The body is oval and laterally compressed and does not flex; instead, the near-symmetrical dorsal and anal fins provide the means of propulsion through 'underwater flight' not dissimilar to that of penguins (Watanabe & Sato, 2008; Watanabe & Davenport, 2021).

Molids were traditionally considered slow, inefficient swimmers (see comments in Cartamil & Lowe, 2004; Watanabe & Sato, 2008), a reputation which likely arose from a combination of their unusual body morphology and the documented M. mola behaviour of 'basking' at the sea-surface to warm up in between deep foraging dives (Cartamil & Lowe, 2004; Nakamura et al., 2015; Nakamura & Yamada, 2022). However, M. mola has an effective locomotive system, with cruise speeds comparable to those of salmonoids and sharks (Watanabe & Sato, 2008; Watanabe & Davenport, 2021). They are also capable of rapid acceleration, with recorded burst speeds for M. mola of 2.2 - 2.4 m/s (Nakamura and Sato, 2014; Watanabe and Sato, 2008) and 6.6 m/s (Thys et al., 2015). A further account describes a M. mola catching a trolled lure towed at 3.6 m/s off Chincoteague, Virginia, USA (Kyle Krabill, pers. comm. 5 August 2020; see also https://www.youtube.com/watch?v=He7NOFfukwc). Further, molids (at least those under two meters) are capable of breaching (Hays et al., 2020; Thys et al., 2020).

Many molid behaviours are not well understood, in particular those that relate to interactions with conspecifics and other taxa, including responses to predators. Due to the extremely large growth spectrum of molids, they presumably rely on different antipredator behaviours and strategies during each life stage. Once molids are past the taxa-specific 'ostracioniform' and 'molacanthiform' early developmental stages, where they are adorned with numerous protective spines (Leis, 1977; Martin & Drewry, 1978; Thys et al., 2020), they presumably rely on fast growth (Nakatsubo & Hirose, 2007; Pan et al., 2016; Pope et al., 2010) to outgrow gape-limited predators. As juveniles

and adults they do not have any obvious defences, and the notion that molids contain tetrodotoxin (Sodeman, 1989), a potent biotoxin used by many marine organisms as a defence against predation (Lorentz et al., 2016), has not been corroborated (Baptista et al., 2020, 2022; Huang et al., 2011; Saito et al., 1991). As adults, they remain potential prey for sealions (Nyegaard et al., 2019; Powell, 2001), orca (Gladstone, 1988; Visser et al., 2023; Visser & Fletcher, 2023), and some species of shark (Fergusson et al., 2000; Nyegaard et al., 2019; Pope et al., 2010). It has been proposed that swift, deep diving may be a response to predators (Cartamil & Lowe, 2004; Sims et al., 2009). Further, breaching in *Mola* has also been suggested to be a response to predators (Thys et al., 2020). However, scant information is available to corroborate these hypotheses and gain a more nuanced picture of molid responses to predators.

During a recent review of interactions between orca Orcinus orca (Linnaeus, 1758) and juvenile/ adult molids (Visser et al., 2023), several unexpected and (to the best of our knowledge) undescribed molid behaviours were observed on video recordings. These behaviours appeared to be attempts to evade the orca and revealed unexpected levels of molid agility. Here we aim to describe these behaviours and illustrate key aspects so that they may be recognised in other contexts. To achieve this, we reviewed video recordings of interactions between orca and molids, examined the molid's reactions to orca, and identified those manoeuvres which repeated between interactions. Here, we present these as descriptions and illustrations, along with examples.

MATERIAL AND METHODS

Sources

We reviewed video recordings from four different orca-molid interactions. The videos were sourced online, but in three instances, the videographers made the original, unedited videos available for this study. In addition, we included a brief offline video in the review, to allow valuable context regarding molid breaching to be presented (Table 1).

For each interaction, the molid species was es-

Interaction	Date	Location	Camera position	Videographer	Source
Mex-2009	11/02/2009	Off Cabo San Lucas, Mexico	Top-side	Michael Van den berg	YouTube ¹
NZ-2013*	02/04/2013	Off Northland, New Zealand	Underwater	Mazdak Radjainia	YouTube ²
SA-2019*	06/03/2019	False Bay, South Africa	Top-side	David Hurwitz	Private
Aus-2020*	05/03/2020	Bremer Canyon, Western Australia	Top-side & underwater	Craig and Stormy, Whale Watch Western Australia	YouTube ³
Mex-2020*	16/07/2020	Off Michoacan and Colima, Mexico	Top-side	Cristobal Alvarez	Online video archive ⁴

Table 1. Orca-molid interactions documented on video and reviewed in this study. *Denotes interactions where the videographers provided the original, unedited video in high resolution for use in this study. Dates are given as dd/mm/yyyy. 1: https://www.youtube.com/watch?v=Yf5MYigV4A0. 2: https://www.youtube.com/watch?v=ocvF9gv5M0s.

tablished to the lowest possible taxonomic level based on the morphology visible on the imagery, following Sawai et al. (2020). Molid size was estimated as Total Length [TL; anterior-most to posterior-most point, following Sawai et al. (2020)], based on the size relative to the orca, combined with a subjective judgement of the molid morphology [Mola spp. change morphology with growth (Nyegaard et al., 2018; Sawai et al., 2018, 2017; Watanabe & Sato, 2008)].

The videos were reviewed in an iterative way, noting behaviours that appeared to be reactions to the orca and which repeated across other videos. The interactions were studied at various video play back speeds, including frame-by-frame, to ascertain if the molids were driving the movements themselves, or if they were influenced by physical contact with the orca (i.e., being nudged, pushed, etc). Only voluntary movements were considered to be molid behaviours.

The behaviours were illustrated and described; 1) as diagrams outlining key aspect of each behaviour, 2) in table format with a brief description of each behaviour and, 3) using a series of frames extracted from the videos to illustrate movement.

RESULTS

The molid species could be ascertained in four interactions, with three *M. alexandrini* and one *M*.

mola identified (Table 2). The fifth molid appeared to be *M. mola*, however, insufficient morphology was visible on the imagery to confirm this. The molids ranged in estimated size from ca. 1–2 m TL (Table 2).

Each of the five videos showed a single molid and multiple orca. The latter circled, approached and harassed the molids, including making physical contact. In turn, the molid reactive behaviours varied, were clearly driven by the molids themselves, and appeared to be attempts to evade the orca and/or discourage the orca from making physical contact. These are shown schematically in Fig. 1, and described in Table 3. The behaviours appeared to (approximately) escalate with orca proximity and are described below in the context of the following scenarios: 1) an orca approaches, but is not yet close enough to make physical contact with the molid; 2)

Interaction name	Molid species	Estimated total length (m)
Mex-2009	Mola mola	2
NZ-2013	Mola alexandrini	1 - 1.2
SA-2019	Mola sp.(likely M. mola)	1.5
Aus-2020	Mola alexandrini	1
Mex-2020	Mola alexandrini	1.5 - 2

Table 2. Species identification and estimated size of molids, determined visually from the video of orca-molid interactions listed in Table 1.

^{3:} https://www.youtube.com/watch?v=wxio3TMNmWI. 4: https://tinyurl.com/MexInt-2020.

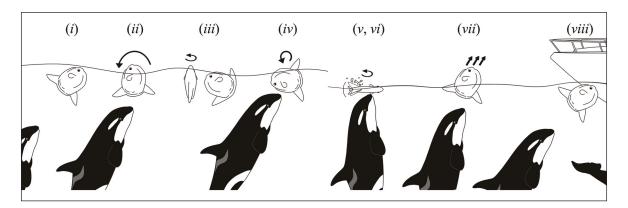


Figure 1. Molid 'Evade' behaviours described in Table 1: (i) 'Seek-surface' and 'Clavus-to-orca', (ii) 'Head-up', (iii) 'Pivot', (iv) 'Ventral-up', (v, vi) 'Spin' and 'Thrash', (vii) 'Breach', and (viii) 'Shelter'. Note these behaviours are not sequential. Illustration by LAF.

Reference to Figure 1	Behaviour term	Description of molid behaviour	Interactions, whe this behaviour woobserved
i	'Seek-surface'	Seek-surface' Stationary (effectively) at the sea surface with the head angled slightly up	
i	'Clavus-to- orca'	Actively keeps the clavus towards the orca	Mex-2009, NZ 2013, Aus-202 Mex-2020
ii	'Head-up'	Abruptly obtains a near-vertical position with the head at or above water	Mex-2009, NZ 2013, Aus-202 Mex-2020
iii	'Pivot'	From 'Head-up', pivots to quickly change direction; or, while upright, quickly changes direction 'on the spot'	Aus-2020, Mes 2020
iv	'Ventral-up'	From 'Head-up', inverts completely so the ventral area is at or above water	NZ-2013, Me 2020
v	'Thrash'	Thrashes at the surface with the dorsal and/or anal fins, without moving forwards	Aus-2020, Mes 2020
vi	'Spin'	While parallel to the surface, spins rapidly	Aus-2020, Mes 2020
vii	'Breach'	Propels itself partially (at least half the body) or fully out of the water	Mex-2020, SA 2019
vii	'Shelter' ¹	Actively positions itself near a vessel (i.e., is not herded towards the vessel by orca), at a distance less than the length of the approaching orca. ¹	Mex-2009, Au 2020

Table 3. Molid 'Evade' behaviours during orca interactions. Interaction names refer to Table 1.

1 Note this behaviour is included here as tentative; see text for details.

the orca is as close as it will get to the molid during the pass (may make physical contact as it passes), and; 3) the orca shows sustained interest and close proximity to the molid, including instances of physical contact.

Approach by orca

When orca approached (as well as in between orca passes), no attempts to dive were observed for the molids in any of the videos. Instead, the molids

repeatedly assumed a stationary position at or very near the sea surface with the head angled slightly upwards (here termed 'Seek-surface'), while actively keeping the clavus towards any close-by orca ('Clavus-to-orca') (*i* in Table 3 and on Figs. 1–4). This position was typically assumed in the early stages of an orca approach.

During an orca pass

As orca approached and neared the point of physical contact, or the point of closest proximity to the molid before passing it, molid behaviours varied. Some reactions included abruptly angling the head upwards and out of the water ('Head-up')

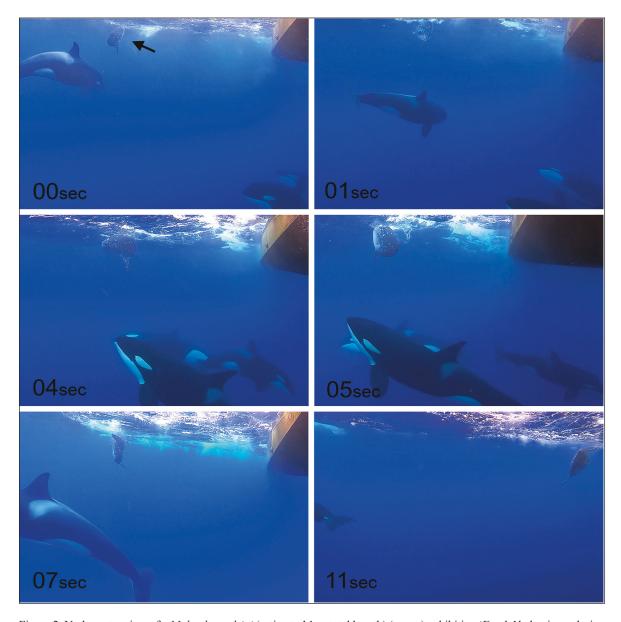


Figure 2. Underwater view of a *Mola alexandrini* (estimated 1 m total length) (arrow) exhibiting 'Evade' behaviours during orca passes. Time elapsed indicated in seconds. The molid assumes the positions 'Seek-surface' and 'Clavus-to-orca', as an orca approaches from the left (Image 1). From here it 'Pivots' to maintain 'Clavus-to-orca' during the pass (Image 2), and also achieves 'Clavus-to-orca' to two 'new' orca approaching from below and to the right (Image 3). As the orca pass directly underneath the molid, it assumes the 'Head-up' position (Image 4), and from here 'Pivots' again to maintain 'Clavus-to-orca' as they continue to the left (Images 5 and 6). Frames from video by Craig, Whale Watch Western Australia (Interaction Aus-2020, Table 1), reprinted with permission.

(ii in Table 3 and on Fig. 1, Fig. 2, Fig. 4). From the 'Head-up' position, a molid would at times 'Pivot' around its own length axis ('Pivot') (iii and on Figs. 1, 2), seemingly to maintain 'Clavus-to-orca' as the orca passed underneath, and/or to prepare to move in the opposite direction to the orca after the pass. This rapid change in direction 'on the spot'

could also be achieved by the molids while in a more upright position, by using their powerful dorsal and anal fins to do so, without moving forwards (e.g., Fig. 3).

Alternatively, from the 'Head-up' position, the molids sometimes continued the backwards motion to briefly invert completely ('Ventral-up') (*iv* in

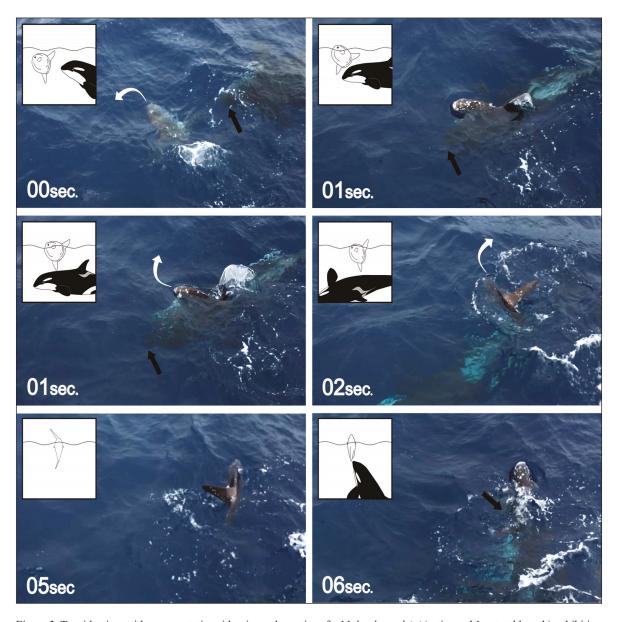


Figure 3. Topside view with representative side-view schematics of a *Mola alexandrini* (estimated 1 m total length) exhibiting 'Evade' behaviours during an orca pass (white arrows denote sunfish turning, black arrows indicate approximate position of the orca's head). Time elapsed indicated in seconds. As an orca approaches (Image 1), the molid quickly 'Pivots' to its left into a 'Head-up' position (Image 2), then immediately turns to the right as the orca passes underneath (Images 3 and 4, respectively), resulting in the molid facing in the opposite direction to the orca (Image 5), ready for 'Head-up' and 'Clavus-to-orca' as the orca turns and approaches again (Image 6). Frames from video by Stormy, Whale Watch Western Australia (Interaction Aus-2020, Table 1), reprinted with permission. Illustrations by LAF.

Table 3 and on Figs. 1 and 4), at times even causing the ventral area to protrude out of the water as the orca passed underneath. The molids would right themselves from this position by simply reversing the 'Head-up', 'Ventral-up' action (not shown here), or right themselves through a side-way twist-like motion (Fig. 4).

Sustained orca interest

During moments of physical interactions, where the orca either nudged the molid, pushed it, or otherwise exhibited sustained interest by maintaining very close proximity, molid behaviours would typically include 'frantic' movements. Specifically, the

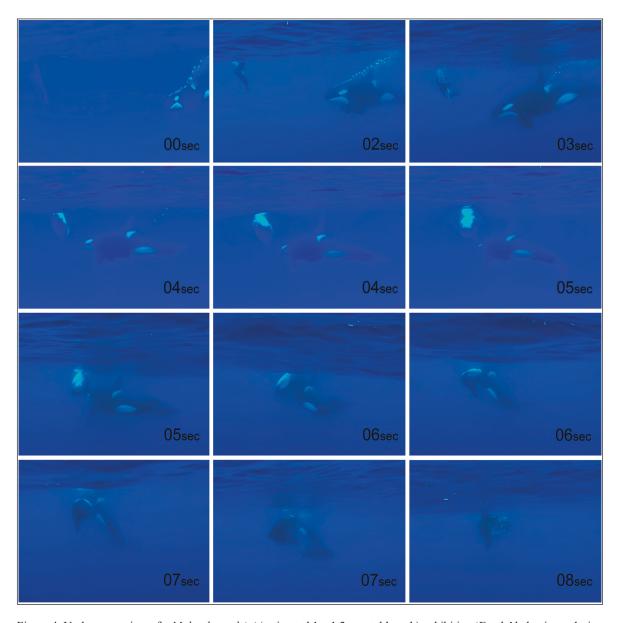


Figure 4. Underwater view of a *Mola alexandrini* (estimated 1 – 1.2 m total length) exhibiting 'Evade' behaviours during an orca pass. Time elapsed indicated in seconds. Prior to the orca approach, the molid is stationary at the sea surface (Image 1). As the orca approaches closer, it assumes the 'Seek-surface' and 'Clavus-to-orca' positions (Images 2 and 3). As the orca gets closer, it assumes the 'Head-up' position (Image 4), directly continuing into the 'Ventral-up' position (Images 5 and 6). From here the molid rights itself by reversing the 'Head-up'-'Ventral-up' movements, with a slight sideways twist (Images 7-12). Frames from video by Mazdak Radjainia, New Zealand (Interaction NZ-2013, Table 1), reprinted with permission.

molids would position themselves flat against the sea surface and spin rapidly around the mid-axis ('Spin') and/or thrash with one or both of the powerful dorsal and anal fins ('Thrash') (*v* in Table 3 and on Figs. 1, 5, 6). When in an upright position, the molids would also use the dorsal fin to 'Thrash' against the sea surface. These behaviours appeared to be attempts to dissuade the orca from making physical contact, although we cannot discount that

they may simply reflect 'panic'. However, in at least one instance an orca clearly recoiled during a 'Thrash' (Fig. 6), providing the molid with an opportunity to then rapidly move forwards and achieve 'Clavus-to-orca'. These actions were therefore – regardless of the intention on behalf of the molid – included here as 'Evade' behaviours.

During some close, sustained interactions with orca, the molids would exhibit an unexpected level

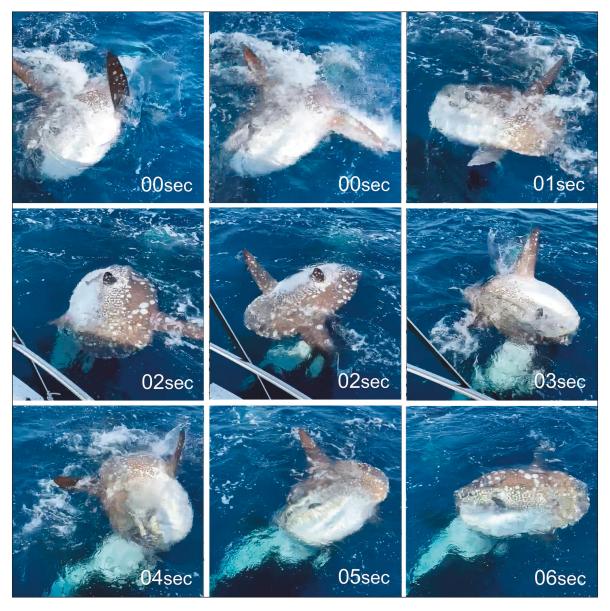


Figure 5. Top-side view of a *Mola alexandrini* (estimated 1.5-2 m total length) exhibiting 'Evade' behaviours during sustained orca interest. Time elapsed indicated in seconds. The molid spins rapidly around its central axis ('Spin') while thrashing with its powerful dorsal and anal fins ('Thrash'), as the orca maintains its position underneath. Frames from video by Cristobal Alvarez (Interaction Mex-2020, Table 1), reprinted with permission.



Figure 6. Top-side view of a *Mola alexandrini* (estimated at 1.5 – 2 m total length) exhibiting the 'Evade' behaviour 'Thrash'. As the orca approaches (upper two images), the molid thrashes with its dorsal fin, causing the orca to recoil (lower two images) and vocalise. Regardless of the intention of the molid, this then provided it with an opportunity to quickly move forwards, past the orca, and achieve the 'Evade' behaviour 'Clavus-to-orca' (not shown). Frames extracted within one second of each other from video by Cristobal Alvarez (Interaction Mex-2020, Table 1), reprinted with permission.

of agility, reacting to the orca with a variety of movements in quick succession, seemingly to attempt to evade physical contact by the orca. One such example is shown in Fig. 7.

Breach

Two different videos showed molids emerging partially from the water (Table 1), indicating they were breaching ('Breach'; *vii* in Table 3 and on Fig. 1). Both videos were recorded from a top-side perspective, rendering the exact context unclear, i.e., if the molids were pushed from below by the orca. However, the brief video from Interaction SA-19 showed a molid breaching in front of two travelling orca, and frame-by-frame analysis of the relative positions strongly suggested that, while the orca were in very close proximity to the molid, they

were too far behind to physically touch it, and could not have pushed it out of the water (Fig. 8).

Close vessel proximity

Finally, we used the term 'Shelter' to describe observations where the molids appeared to use the side of the vessel to shelter from orca (*viii* in Table 3 and on Fig.1). Naturally, as all the observations were made from vessels, any proximity may have been purely coincidental. However, in one interaction, the molid appeared to actively seek the side of the vessel (Fig. 9), and another interaction, where similar behaviour was documented (Fig. 2), the interaction was described by the observers as: "They [i.e., the orca] began to push him [i.e., the molid] closer to us and within sight of the boat, little Sunfish tried to swim towards us for a distraction but

each time the Orca pushed him back." (Whale Watch Australia, 2020). A third interaction showed extensive, close interactions up against the hull of the vessel (Fig. 7), however, in this case it was unclear if the molid had actively positioned itself near

the vessel, if it had been herded there by the orca, or if the proximity was purely coincidental.

We have included 'Shelter' here as a tentative 'Evade' behaviour, although we acknowledge it may not always be deliberate on behalf of the



Figure 7. Top-side view of a *Mola alexandrini* (estimated at 1.5-2 m total length), performing a series of 'Evade' maneuverers in quick succession in reaction to the approach of two orca cooperatively hunting [see also Visser et al. (2023)]. Time elapsed indicated in seconds. The molid first exhibits 'Head-up' (Image 1), then immediately 'Pivots' seemingly to avoid physical contact by the orca (Images 3, 4). The molid then rolls backwards into 'Ventral-up' (Image 5), then immediately continues the backwards motion with a side-way twist (Images 6-8) to right itself, ending up side-ways to the orca, which is moving forwards (Image 9). The molid immediately twists its backend upwards and sideways over the head of the orca (Images 10-14), clearing the orca (Image 15), ending in 'Ventral-up' (Image 16). The molid immediately rights itself with a side-way twist (Images 17, 18), then 'Thrashes' directly onto the second orca, which is now approaching (Images 19, 20). Frames extracted from video by Cristobal Alvarez (Interaction Mex-2020, Table 1), reprinted with permission.

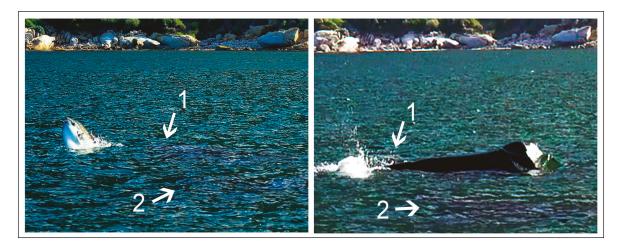


Figure 8. Top-side view of a *Mola* sp. (likely *M. mola*) (estimated 1.5 m total length) exhibiting the 'Evade' behaviour 'Breach' in front of two orca travelling underwater. The arrows indicate the approximate location of each orca's head, i.e., neither was within range of the molid at the moment of breaching, indicating the molid was not pushed out of the water by the orca. Note the dorsal fin of orca #1 is collapsed to the left side. Frames extracted within one second of each other from video by David Hurwitz (Interaction SA-2019, Table 1), reprinted with permission.

molid, and could even potentially be detrimental if the molid gets 'trapped' between the vessel and the orca. We consider 'Shelter' to be achieved when the molid is within one orca body length of the vessel, as at this point the orca's ability to manoeuvre and approach at the surface is limited by the physical presence of the vessel. However, importantly, for inclusion into this category of behaviour, the molid needs to have assumed this position itself without having been herded there by orca.

DISCUSSION

The observations described here revealed unexcepted levels of molid agility during interactions with orca. Although the traditional view of molids as slow and cumbersome swimmers has been disproved (Cartamil & Lowe, 2004; Watanabe & Davenport, 2021), the variety of manoeuvres and quick reactions to orca were still surprising to us. The observations do, however, corroborate descriptions of captive molids as "...surprisingly agile and can swim backwards away from unknown foreign objects" by Howard et al. (2020).

It is in some ways also surprising that the molid manoeuvres described here have gone unnoticed as all but one of the reviewed videos are available online. One explanation may be a possible predisposition by observers to interpret orca-molid interactions based on the assumption of molid sluggishness, so that any molid movement is perceived as a result of physical pushing by orca. A social media comment to Interaction Mex-2009 exemplifies this: "Sunfish tend to not react to any kind of pain or trauma and won't even make an attempt to escape predators, its like watching a cabbage get chopped up". The findings of our study strongly suggest otherwise; careful frame-by-frame video analysis, tracking molid and orca positions relative to one another, corroborated that the molids drive the movements themselves, that they certainly react to orca, and appear to make concerted efforts to evade them. They are of course not always successful (Visser et al., 2023), but this is a fate they have in common with a large variety of other taxa, which also fall prey to orca (e.g., Ford, 2019; Visser et al., 2023).

The observed molid behaviours appeared to be attempts to evade physical contact, and/or keep the head and ventral area away from the orca, and/or present the clavus to them. Due to the unusual molid locomotor system powered by the dorsal and anal fins, rather than movement of a caudal fin (Watanabe & Sato, 2008; Watanabe & Davenport, 2021), sunfish can survive with large parts of the clavus missing (e.g., Nyegaard et al., 2019). The

'Evade' behaviours may have evolved to present the least vulnerable body part to the threat, while keeping the head and ventral area away, where an orca bite would presumably be fatal.

It is not clear from the videos if the 'Evade' behaviours overall increase the chance of survival for molids when targeted by orca, as many interactions still conclude with the demise of the molid (Visser et al., 2023). However, similar 'Evade' behaviours were seen in both *M. alexandrini* and *M. mola*, as well as in *M. alexandrini* from different ocean basins. This suggests the behaviours are not learnt, but have evolved in at least two species of *Mola*, and presumably play a role in decreasing the risk of falling prey to orca.

One could speculate that a more effective reaction to the presence of orca would be for molids to dive rapidly to great depths. Molids have been recorded to dive to over 1,100 m (Chang et al., 2021; Thys et al., 2017), and while orca can dive to similar depths (Towers et al., 2019) they are restricted in their need to breathe air. Abrupt, deep diving has indeed been recorded during telemetry studies on M. mola, and has been suggested to be a reaction to predators (Cartamil & Lowe, 2004). Similarly, rare video of Lamalera whale hunters in Indonesia shows an attempt by a M. alexandrini harpooned at the surface to dive straight down (Palička, 2016). It is therefore puzzling why the molids on the reviewed videos did not attempt to dive. It is possible they had already failed in such an attempt and were now 'trapped' by the orca in surface waters, and/or that escape attempts were yet to come. It is also possible the behaviour of the molids and/or the orca may have been influenced by the presence of humans — an important factor to consider in observational studies.

Overall, further studies are needed to better understand orca-molid interactions and how they escalate (e.g., Visser et al., 2023), as well as how molids react to other predators and overall decrease the risk of predation. Regardless, the observed behaviours described herein illustrate that molids react to orca with apparent evasive manoeuvres, that they possess notable levels of agility and quick reaction times, and that they are far from sluggish creatures.

ACKNOWLEDGEMENTS

We acknowledge Māori as tangata whenua and Treaty of Waitangi partners in Aotearoa New Zealand. We thank Haze Sommer for her help with sourcing videos online. The following kindly made video and contextual information available: Cristobal Alvarez, David Hurwitz, Mazdak Radjainia and Whale Watch Western Australia (Craig and Stormy). We also acknowledge Michael Van den berg for the use of his video uploaded to YouTube. We thank Diane Fraleigh, Natasha Philips and Krista van der Linde for their reviews and suggested edits which improved the manuscript. INV thanks her Patreon supporters for their financial assistance during the preparation of this publication.

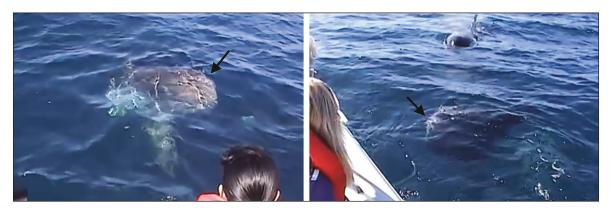


Figure 9. Top-side view of a *Mola mola* (estimated 2 m total length) appearing to actively position itself in close proximity to the vessel ('Shelter') with the head angled upwards at the surface ('Seek-surface'), and the clavus facing outwards towards the orca ('Clavus-to-orca'). Arrow indicates the mouth (i.e., front end) of the molid. Still images extracted within 17 seconds of each other from video by Michael Van den berg, Mexico (Interaction Mex-2009, Table 1), reprinted under YouTube fair use guidelines.

REFERENCES

- Baptista M., Braga A.C., Rosa R. & Costa P.R., 2022. Does ocean sunfish *Mola* spp. (Tetraodontiformes: Molidae) represent a risk for tetrodotoxin poisoning in the Portuguese Coast? Marine Drugs, 20: 594. https://doi.org/10.3390/md20100594
- Baptista M., Figueiredo C., Lopes C., Costa P.R., Dutton J., Adams D.H., Rosa R. & Raimundo J., 2020. Biotoxins, trace elements, and microplastics in the ocean sunfishes (Molidae). In: Tierney M.T., Hays G.C. & Houghton J.D.R. (Eds.), The ocean sunfishes, evolution, biology and conservation. CRC Press, Boca Raton, pp. 186–215. https://doi.org/10.1201/9780429343360-11.
- Britz R., 2022. Comments on the holotype of *Orthragoriscus alexandrini* Ranzani 1839 (Teleostei: Molidae). Zootaxa, 5195: 391–392. https://doi.org/10.11646/zootaxa.5195.4.6.
- Cartamil D.P. & Lowe, C.G., 2004. Diel movement patterns of ocean sunfish *Mola mola* off southern California. Marine Ecology Progress Series 266: 245–253. https://doi.org/10.3354/meps266245.
- Chang C.T., Chiang W.C., Musyl M.K., Popp B.N., Lam C.H., Lin S.J., Watanabe Y.Y., Ho Y.H. & Chen J.R., 2021. Water column structure influences long-distance latitudinal migration patterns and habitat use of bumphead sunfish *Mola alexandrini* in the Pacific Ocean. Scientific Reports 11: 21934. https://doi.org/10.1038/s41598-021-01110-y
- Fergusson I.K., Compagno L.J.V. & Marks M.A., 2000. Predation by white sharks *Carcharodon carcharias* (Chondrichthyes: Lamnidae) upon chelonians, with new records from the Mediterranean Sea and a first record of the ocean sunfish *Mola mola* (Osteichthyes: Molidae) as stomach contents. Environmental Biology of Fishes, 58: 447–453. https://doi.org/10.1023/A:1007639324360.
- Ford J.K.B. 2019. Chapter 11 Killer Whales: Behavior, social organization, and ecology of the oceans' apex predators. In: Würsig B. (Ed.), Ethology and Behavioral Ecology of Odontocetes. Springer, Switzerland, 239-259.
 - https://doi.org/10.1007/978-3-030-16663-2 11.
- Fraser-Brunner A., 1951. The ocean sunfishes (Family Molidae). Bulletin of the British Museum (Natural History) Zoology, 1: 87–121. https://doi.org/10.5962/bhl.part.21630.
- Fricke R., Eschmeyer W.N. & van der Laan R., 2022 version of 4 Oct 2022. Eschmeyer's catalog of fishes. https://www.calacademy.org/scientists/projects/eschmeyers-catalog-of-fishes (accessed 11 Oct 2022).
- Gladstone W., 1988. Killer whale feeding observed underwater. Journal of Mammalogy, 69: 629–630. https://doi.org/10.2307/1381360

- Gomes-Pereira J., Pham C., Catarino D., Miodonsky J., Santos M.A.R., Dionísio G., Nyegaard M., Sawai E. & Afonso P., 2022. The heaviest bony fish in the world: a 2744 kg giant sunfish *Mola alexandrini* (Ranzani, 1839) from the North Atlantic. Journal of Fish Biology, 101: 1–4. https://doi.org/10.1111/jfb.15244
- Hays G.C., Houghton J.D.R., Thys T.M., Adams D.H., Ahuir-Baraja A.E., Alvarez J., Baptista M., Batista H., Baylina N., Bemis K.E., Bemis W.E., Caldera E.J., Carnevale G., Carson C.D., Correia J.P., Costa P.R., Daly O., Davenport J., Dutton J., Eagling L.E., Figueiredo C., Forsgren K., Freese M., García-Barcelona S., Harrod C., Hearn A., Hellenbrecht L., Hilton E.J., Howard M.J., Kelly R., Kubicek L., Lopes C., Mowatt-Larssen T., McBride R., Nakamura I., Nakatsubo T., Nixon E., Nyegaard M., Ostalé-Valriberas E., Pellegrino L., Phillips N.D., Pope E.C., Potter I., Raimundo J., Riis M., Rosa R., Ryan J.P., Sawai E., Shinohara G., Sims D.W., Sousa L.L., Taura C., Tholke E., Tsukamoto K., Tyler J.C., Watanabe Y.Y., Weng K.C., Whitney J.L., Yamanoue Y. & Ydesen K.S.,. 2020. Unresolved Questions About Ocean Sunfishes, Molidae: A Family Comprising Some of the World's Largest Teleosts. In: Thys T.M., Hays G.C., Houghton J.R. (Eds.), The Ocean Sunfishes. Evolution, Biology and Conservation. CRC Press, Boca Raton, pp. 280-296. https://doi.org/10.1201/9780429343360-15
- Howard M.J., Nakatsubo T., Correira J.P., Batista H., Baylina N., Taura C., Ydesen K.S. & Riis M., 2020.
 Sunfish on display. Husbandry of the ocean sunfish *Mola mola*. In: Thys T.M., Hays G.C. & Houghton J.R. (Eds.), The Ocean Sunfishes. Evolution, Biology and Conservation. CRC Press, Boca Raton, pp. 242–261.
- Huang K.M., Liu S.M., Huang Y.W., Huang K.L. & Hwang D.F., 2011. Food poisoning caused by sunfish *Masturus lanceolatus* in Taiwan. Journal of Food and Drug Analysis, 19: 191–196. https://doi.org/10.38212/2224-6614.2243.
- Johnson G.D. & Britz R., 2005. Leis' conundrum: homology of the clavus of the ocean sunfishes. 2. Ontogeny of the median fins and axial skeleton of *Ranzania laevis* (Teleostei, Tetraodontiformes, Molidae). Journal of Morphology, 266: 11–21. https://doi.org/10.1002/jmor.10242
- Leis J.M., 1977. Development of the eggs and larvae of the slender mola, *Ranzania laevis* (Pisces, Molidae). Bulletin of Marine Science, 27: 448–466.
- Lorentz M.N., Stokes A.N., Rößler D.C., Lötters S., 2016. Tetrodotoxin. Current Biology, 26: R870–R872. https://doi.org/10.1016/j.cub.2016.05.067
- Martin F.D. & Drewry G.E., 1978. Development of fishes of the mid-Atlantic Bight: An atlas of egg, lar-

- val, and juvenile stages, Vol VI Stromateidae through Ogcocephalidae. Fort Collins, US Fish and Wildlife Service, US Department of the Interior.
- Nakamura I., Goto Y. & Sato K., 2015. Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. Journal of Animal Ecology, 84: 590–603. https://doi.org/10.1111/1365-2656.12346
- Nakamura I. & Sato K., 2014. Ontogenetic shift in foraging habit of ocean sunfish *Mola mola* from dietary and behavioral studies. Marine Biology, 161: 1263– 1273
 - https://doi.org/10.1007/s00227-014-2416-8
- Nakamura I. & Yamada M., 2022. Thermoregulation of ocean sunfish in a warmer sea suggests their ability to prevent heat loss in deep, cold foraging grounds. Journal of Experimental Marine Biology and Ecology, 546: 151651.
 - https://doi.org/10.1016/j.jembe.2021.151651
- Nakatsubo T. & Hirose H., 2007. Growth of captive ocean sunfish, *Mola mola*. Aquaculture Science, 55: 403–407.
 - https://doi.org/10.11233/aquaculturesci1953.55.403
- Nyegaard M., Andrzejaczek S., Jenner C.S. & Jenner M.N.M., 2019. Tiger shark predation on large ocean sunfishes (Family Molidae) two Australian observations. Environmental Biology of Fishes, 102: 1559–1567.
 - https://doi.org/10.1007/s10641-019-00926-y
- Nyegaard M., Sawai E., Gemmell N., Gillum J., Loneragan N.R., Yamanoue Y. & Stewart A.L., 2018. Hiding in broad daylight: molecular and morphological data reveal a new ocean sunfish species (Tetraodontiformes: Molidae) that has eluded recognition. Zoological Journal of Linnean Society, 82: 631–658. https://doi.org/10.1093/zoolinnean/zlx040
- Palička J., 2016. Whale Hunters from Lamalera Part 6 Hunt. *Mola Mola* / Velrybáři z Lamalery - 6 Měsíčník.
 - https://www.youtube.com/watch?v=Hxxu5xxzkXo
- Pan, H., Yu, H., Ravi, V., Li, C., Lee, A.P., Lian, M.M., Tay, B.-H., Brenner, S., Wang, J., Yang, H., Zhang, G., Venkatesh, B., 2016. The genome of the largest bony fish, ocean sunfish (*Mola mola*), provides insights into its fast growth rate. Gigascience 5: 36. https://doi.org/10.1186/s13742-016-0144-3.
- Pope E.C., Hays G.C., Thys T.M., Doyle T.K., Sims D.W., Queiroz N., Hobson V.J., Kubicek L. & Houghton J.D.R., 2010. The biology and ecology of the ocean sunfish *Mola mola*: A review of current knowledge and future research perspectives. Reviews in Fish Biology and Fisheries, 20: 471–487. https://doi.org/10.1007/s11160-009-9155-9
- Powell, D.C., 2001. A fascination for fish: adventures of an underwater pioneer. University of California Press, Berkeley and Los Angeles.

- Saito T., Noguchi T., Shida Y., Abe T., Hashimoto K., 1991. Screening of tetrodotoxin and its derivatives in puffer-related species. Nippon Suisan Gakkaishi 57: 1573–1577. https://doi.org/10.2331/suisan.57.1573.
- Sawai E. & Nyegaard M., 2022. A review of giants: examining the species identities of the world's heaviest extant bony fishes (ocean sunfishes, family Molidae). Journal of Fish Biology, 100: 1345–1364. https://doi.org/10.1111/jfb.15039.
- Sawai E., Nyegaard M. & Yamanoue Y., 2020. Phylogeny, taxonomy and size records of ocean sunfishes. In: Thys M.T., Hays G.C. & Houghton J.D.R. (Eds.), The ocean sunfishes, evolution, biology and conservation. CRC Press, Boca Raton, pp. 18–36. https://doi.org/10.1201/9780429343360-2
- Sawai E., Yamanoue Y., Jawad L., Al-Mamry J. & Sakai Y., 2017. Molecular and morphological identification of *Mola* sunfish specimens (Actinopterygii: Tetraodontiformes: Molidae) from the Indian Ocean. Species diversity, 22: 99–104. https://doi.org/10.12782/sd.22_99.
- Sawai E., Yamanoue Y., Nyegaard M. & Sakai Y., 2018. Redescription of the bump-head sunfish *Mola alexandrini* (Ranzani 1839), senior synonym of *Mola ramsayi* (Giglioli 1883), with designation of a neotype for *Mola mola* (Linnaeus 1758) (Tetraodontiformes: Molidae). Ichthyological Research, 65: 142–160. https://doi.org/10.1007/s10228-017-0603-6.
- Sims D.W., Queiroz N., Doyle T.K., Houghton J.D.R. & Hays G.C., 2009. Satellite tracking of the World's largest bony fish, the ocean sunfish (*Mola mola* L.) in the North East Atlantic. Journal of Experimental Marine Biology, 370: 127–133.
 - https://doi.org/10.1016/j.jembe.2008.12.011.
- Thys T.M., Hearn A.R., Weng K.C., Ryan J.P., Peñaher-rera-Palma C., 2017. Satellite tracking and site fidelity of short ocean sunfish, *Mola ramsayi*, in the Galapagos Islands. Journal of Marine Biology, 2017: 7097965. https://doi.org/10.1155/2017/7097965
- Thys T. M., Nyegaard M. & Kubicek L., 2020. Ocean sunfishes and society. In: Thys T.M., Hays G.C. & Houghton J.D.R. (Eds.), The Ocean Sunfishes. Evolution, Biology and Conservation. CRC Press, Boca Raton, pp. 262–279.
 - https://doi.org/10.1201/9780429343360-14
- Thys T.M., Nyegaard M., Whitney J.L., Ryan J.P., Potter I., Nakatsubo T., Freese M., Hellenbrecht L.M., Kelly R., Tsukamoto K., Shinohara G., Mowatt-Larssen T. & Kubicek L., 2020. Ocean sunfish larvae. In: Thys T.M., Hays G.C. & Houghton J.D.R. (Eds.), The Ocean Sunfishes. CRC Press, Boca Raton, pp. 105–128. https://doi.org/10.1201/9780429343360-7
- Thys T.M., Ryan J.P., Dewar H., Perle C.R., Lyons K., O'Sullivan J., Farwell C., Howard M.J., Weng K.C.,

- Lavaniegos B.E., Gaxiola-Castro G., Miranda Bojorquez L.E., Hazen E.L. & Bograd S.J., 2015. Ecology of the ocean sunfish, *Mola mola*, in the southern California Current System. Journal of Experimental Marine Biology and Ecology, 471: 64–76. https://doi.org/10.1016/j.jembe.2015.05.005.
- Thys T.M., Hays G.C. & Houghton J.D.R., 2020. The Ocean Sunfishes: Evolution, Biology and Conservation, 1st ed. CRC Press, Boca Raton. https://doi.org/10.1201/9780429343360
- Towers J.R., Tixier P., Ross K.A., Bennett J., Arnould J.P.Y., Pitman R.L. & Durban J.W., 2019. Movements and dive behaviour of a toothfish-depredating killer and sperm whale. ICES Journal of Marine Science, 76: 298–311.
 - https://doi.org/10.1093/icesjms/fsy118
- Visser I.N. & Fletcher L.A., 2023. First records of orca, Orcinus orca (Linnaeus, 1758) (Mammalia Cetacea), predation on sharptail ocean sunfish, Masturus lanceolatus (É. Liénard, 1840) (Pisces Molidae), with novel components of foraging behaviour discovered through

- social media.Biodiversity Journal, 14: 19–60. https://doi.org/10.31396/Biodiv.Jour.2023.14.1.19.60
- Visser I.N., Nyegaard M. & Fletcher L.A., 2023. Orca, Orcinus orca (Linnaeus, 1758) (Mammalia Cetacea) interactions with ocean sunfishes (Family Molidae, genus Mola Kölreuter, 1766 and Masturus Gill, 1884): A global review. Biodiversity Journal, 14: 61– 164.
- https://doi.org/10.31396/Biodiv.Jour.2023.14.1.63.166 Watanabe Y. & Sato K., 2008. Functional dorsoventral symmetry in relation to lift-based swimming in the ocean sunfish *Mola mola*. PLoS One 3: e3446. https://doi.org/10.1371/journal.pone.0003446
- Watanabe Y.Y. & Davenport J., 2021. Locomotory Systems and biomechanics of ocean sunfish. In: Thys T.M., Hays G.C. & Houghton J.D.R. (Eds.), The Ocean Sunfishes. CRC Press, Boca Raton, pp. 72–86. https://doi.org/10.1201/9780429343360-5
- Whale Watch Australia, 2020. Orca play with sunfish. https://www.youtube.com/watch?v=wxio3TMNmWI&t =3s (accessed 11 Oct 2022)

