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RESEARCH

Tool use by New World *Halichoeres* wrasses

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Abstract A diverse array of animals has evolved the ability to use tools (e.g., primates, parrots, octopus, crabs, and wasps), but the factors leading to tool use evolution are poorly understood. Fishes could provide insight into these factors via comparison of ecological and morphological differences between tool-using and non-tool-using species. Anvil use is one example of tool use by fish: the fish holds a hard-shelled prey item in its mouth and strikes it onto a hard surface (anvil) to open it. To date, anvil use has been described in 26 of the > 550 described wrasse/Labridae species. Through a community science program called *Fish Tool Use*, 16 new observations of anvil use were collected in five species of a monophyletic group of wrasses called the New World *Halichoeres*. These new observations provide the first evidence of anvil use by *Halichoeres brasiliensis*, *H. poeyi* and *H. radiatus*, and the first video evidence of anvil use by *H. garnoti* and *H. bivittatus.* They extend the geographic range of known anvil use by wrasses to a new region, the western Atlantic, making this behaviour even more widespread than previously reported. Video analysis revealed that wrasses are flexible in their anvil use: They did not have a preferred side of their body, they cracked open a diverse array of prey on a variety of anvil types, and often used many anvils and striking points for the same prey item. More observations are needed to determine the evolutionary origin of anvil use behaviour, its ecological drivers, costs, and benefits.

Keywords Labridae · Anvil use · Foraging · Predation · Western Atlantic · Feeding behaviour

Introduction

Tool use was once thought to be a uniquely human trait and play a fundamental role in human evolution. Evidence now suggests that tool use is widespread among animals (Shumaker et al. 2011). An animal is using a tool when it uses an external object to accomplish a particular task (Van Lawick-Goodall 1971), such as when some capuchin monkeys use stones to crack open nuts (Barrett et al. 2018). Using a tool allows the animal to achieve the task or do so more easily. Tool use appears to be highly beneficial to animals, raising the question of why all animals do not use tools. To answer this question, we need to unravel the factors that drive the evolution of this behaviour. There is some evidence from comparative studies that tool use evolution is explained by ecological, cognitive, and physical factors. In capuchin monkeys, populations using tools tend to be less exposed to predation than populations not using tools (Barrett et al. 2018) and in woodpecker finches and sea otters, populations using tools are found in environments where the food accessible without tools is scarce or unpredictable (Tebbich et al. 2002; Fujii et al. 2017). In contrast, some studies on primates have failed to find any ecological factors associated with the evolution of tool use (Furuichi et al. 2015; Fox et al. 2004). Tool use may also be part of an 'intelligence' syndrome in primates and birds. Primates and bird species which use tools tend to also innovate more, learn from other individuals more often,

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and have larger brains than species which do not use tools (Reader and Laland 2002; Lefebvre et al. 2004). Finally, New Caledonian crows have a bill shape and binocular vision that seems to allow these birds to use and craft tools, while closely-related species cannot (Troscianko et al. 2012). Although these comparative studies provide hints as to some of the potential evolutionary drivers of tool use, more data are needed to confirm or refute these hypotheses. The study of the evolution of tool use to date has been limited by the difficulty in finding closely-related populations or species with varying degrees of tool use and contrasting morphology and ecology. Though poorly studied, tool use in fish could be an exception as fish is the most specious vertebrate group with high ecological and morphological diversity, sometimes even between closely-related species.

Anvil use is one example of tool use in fish (Brown 2012). When using an anvil, a fish will (i) grab a hard-shelled prey item such as an urchin or a bivalve in its mouth, (ii) swim to a hard surface such as a rock or coral head, and (iii) strike the prey item quickly and repeatedly on the hard surface until it breaks open (Fig. 4). Anvil use has been described in 26 fish species, all wrasses belonging to the family Labridae (Table 1, Fig. 1). Labridae is the second most speciose family of marine fish with 564 described species in FishBase (accessed April 2024), making it a promising clade with which to carry out a comparative analysis of species with varying degrees of anvil use. However, we first need to collect more information about this behaviour, particularly regarding the species and geographic locations in which it occurs. At the moment, information about anvil use is limited for most species, typically consisting of only two lines of description of the behaviour in a paper focusing on another topic or a single video of one individual using an anvil at a single location (but see some detailed work conducted by Pryor and Milton on *Choerodon graphicus*; Table 1).

Gathering information about anvil use in fish can also inform us about the cognitive skills required for tool use, namely laterality and the process of tool selection. There is evidence that tool use is a strongly lateralised behaviour: primates and New Caledonian crows manipulate tools with a preferred hand or claw (Rutledge and Hunt 2004). This suggests that laterality could be necessary for the emergence of tool use and the evolution of complex manipulatory behaviours more generally (Brown and Magat 2011). There is evidence that animals select objects to use as tools on their basis of certain physical properties, enabling them to successfully complete the task and avoiding the need to try out many different objects on the task before finding the right one (e.g. capuchin monkeys, Manrique et al. 2011; New Caledonia crows, Klump et al. 2019; ants, Maák et al. 2017). Wrasses have been observed using all sorts of hard surfaces as anvils, mainly rocks and corals but also the side of the aquarium and human-made objects (references in Table 1). This suggests that they are quite flexible in their anvil selection and they might have a good understanding of the properties (hardness) of surfaces in their environment. Some papers have also described that the wrasse seemed to swim towards a specific rock or the presence of a midden (i.e. a small pile) of broken shells around the anvil, suggesting that some wrasses have preferred anvils (Bernardi 2012; Pryor 2020).

We initiated a community science program, called *Fish Tool Use*, to gather observations of fish anvil use from around the world. In this paper, we describe 16 new observations of anvil use documented by participants in this program. These observations describe anvil use in five species belonging to a clade of wrasses called the New World *Halichoeres*. The monophyly of the New World *Halichoeres* clade has been supported by all Labridae phylogenies (Barber and Bellwood 2005; Cowman and Bellwood 2011; Baliga and Law 2016; Rabosky et al. 2018; Wainwright et al. 2018; Hughes et al. 2023). The New World *Halichoeres* clade contains a total of 20 species in the phylogeny of the Fish Tree of Life (Rabosky et al. 2018), one of the most complete Labridae phylogenies with 339 Labridae species included. The precise number of species in the clade is unknown as the *Halichoeres* genus is the most polyphyletic genus in the Labridae family, with at least eight independent branches (Fig. 1). This clade diverged between 21.2 and 18.1 million years ago from a common wrasse ancestor (Barber and Bellwood 2005). As its name suggests, the clade comprises species of the genus *Halichoeres* (and one *Oxycheilinus*), all of which are found in the Caribbean and Western Atlantic Ocean. To determine their phylogenetic relationship to other members of the New World *Halichoeres* group and to the other tool-using wrasses, we first plotted the five species on the phylogenetic tree of Labridae. We also plotted the locations of observations on a world map to assess if anvil use was restricted to a specific region, aiming to identify ecological factors associated with the occurrence of anvil use. We finally conducted detailed video analysis to assess the laterality of anvil use, anvil selection, and other aspects related to the costs and benefits of anvil use in fish.

Material and methods

An anvil use event was defined as a fish taking a prey item in its mouth and striking it on a hard surface. To gather observations of anvil use from around the world, we have been running a community science program called *Fish Tool Use*. To raise awareness of the project and encourage people to send us their observations, we sent emails to researchers and various marine biology organisations and posted on social media, particularly Instagram and

Table 1 Evidence of anvil use in fish in the literature

Species	Common name	Level of evidence	Location observation	Prey	Species repartition	Paper
Cheilinus fasciatus	Red-breasted wrasse	Description in a paper on another subject	Eilat. Israel. Red Sea	Sea urchin	Indo-Pacific	Fricke (1971)
Cheilinus lunuatus	Broomtail wrasse	Description in a paper on another subject	Eilat. Israel. Red Sea	Sea urchin	Western Indian Ocean	Fricke (1971)
Cheilinus trilobatus	Tripletail wrasse	Description in a paper on another subject	Eilat. Israel. Red Sea	Sea urchin	Indo-Pacific	Fricke (1973)
Choerodon anchorago	Orange-dotted tuskfish	Video of one individual at a single location	Palau. Micronesia. West Pacific Ocean	Bivalve	Indo-West Pacific	Bernardi (2012)
Choerodon cyanodus	Blue tuskfish	Video of one individual at a single location	Heron Island. Australia. West Pacific Ocean	Juvenile turtle	Indo-West Pacific	Harbone and Tholan (2016)
Choerodon graphicus	Graphic tuskfish	Video of multiple individuals at a single location	Ilot Maitre. New Caledonia. West Pacific Ocean	Bivalve	Western Pacific	Pryor and Milton (2019)
Choerodon graphicus	Graphic tuskfish	Video of multiple individuals at a single location	Ilot Maitre. New Caledonia. West Pacific Ocean	Hard-shelled molluscs	Western Pacific	Pryor and Milton (2021)
Choerodon graphicus	Graphic tuskfish	Videos of multiple individuals at different locations	Nouméa. New Caledonia. West Pacific Ocean	Sea urchin	Western Pacific	Pryor and Milton (2023)
Choerodon graphicus	Graphic tuskfish	Video of multiple individuals at a single location	Ilot Maitre. New Caledonia. West Pacific Ocean	Hard-shelled molluscs	Western Pacific	Pryor (2020)
Choerodon schoenleinii	Blackspot tuskfish	Pictures of one individual at a single location	Keppel region. Australia. West Pacific Ocean	Bivalve	Indo-West Pacific	Jones et al. (2011)
Coris aygula	Clown coris	Description in a paper on another subject	Eilat. Israel. Red Sea	Sea urchin	Indo-Pacific	Fricke (1971)
Coris aygula	Clown coris	Description in a paper on another subject	Eilat. Israel. Red Sea	Sea urchin	Indo-Pacific	Fricke (1973)
Coris bulbifrons	Doubleheader	Video of one individual at a single location	Lord Howe Island. Australia. West Pacific Ocean	Crab	Southwest Pacific	Pryor (2022)
Coris dorsomacula	Pale-barred coris	Description in a paper on another subject	Miyake Island. Japan. Philippine Sea	Unknown	Western Pacific	Tribble (1982)
Coris julis	Mediterranean rainbow wrasse	Description in a paper on another subject	Scandola. France; Cabrera, Medes Islands. Spain; Mediterranean sea	Sea urchin	Eastern Atlantic, Mediterranean	Sala (1997)
Coris julis	Mediterranean rainbow wrasse	Description in a paper on another subject	Banyuls sur mer. France. Mediterranean sea	Crab	Eastern Atlantic, Mediterranean	Wirtz and Diesel (1983)
Coris julis	Mediterranean rainbow wrasse	Description in a paper on anvil use	Banyuls sur mer. France. Mediterranean sea	Crab	Eastern Atlantic, Mediterranean	Wirtz (1996)

Table 1 (continued)

Species	Common name	Level of evidence	Location observation	Prey	Species repartition	Paper
Coris sandeyeri	Sandager's wrasse	Description in a paper on another subject	Goat Island Bay near Leigh. New Zealand. Southwest Pacific Ocean	Isopod	Southwest Pacific	Ayling and Grace (1971)
Halichoeres bivittatus	Slippery dick	Description in a paper on another subject	Carrie Bow Cay. Belize. Caribbean Sea	Crab	Western Atlantic	Wainwright (1988)
Halichoeres garnoti	Yellowhead wrasse	Description in a paper on anvil use	Conch Reef. USA. West Atlantic Ocean	Bivalve	Western Atlantic	Coyer (1995)
Halichoeres garnoti	Yellowhead wrasse	Description in a paper on another subject	Carrie Bow Cay. Belize. Caribbean Sea	Crab	Western Atlantic	Wainwright (1988)
Halichoeres hortulanus	Checkerboard wrasse	Video of multiple individuals at a single location	Lakshadweep Archipelago. India. Indian Ocean	Sea urchin	Indo-Pacific	Jaishankar et al. (2024)
Halichoeres maculipinna	Clown wrasse	Description in a paper on another subject	Carrie Bow Cay. Belize. Caribbean Sea	Crab	Western Atlantic	Wainwright (1988)
Lachnolaimus maximus	Hogfish	Description in a paper on another subject	Florida Keys. USA. West Atlantic Ocean	Sea urchin	Western Atlantic	Phillips (1964)
Pseudolabrus luculentus	Orange wrasse	Video of one individual at a single location	Lord Howe Island. Australia. West Pacific Ocean	Crab	Southwest Pacific	Pryor (2022)
Pseudolabrus miles	Scarlet wrasse	Description in a paper on another subject	Aquarium	Crab	Southwest Pacific	Hazlett and McLay (2000)
Semicossyphus pulcher	California sheephead	Video of multiple individuals at a single location	Point Loma. USA. East Pacific Ocean	Sea urchin	Eastern Pacific	Dunn (2016)
Symphodus mediterraneus	Axillary wrasse	Description in a paper on another subject	Banyuls sur mer. France. Mediterranean sea	Crab	Eastern Atlantic, Mediterranean	Wirtz and Diesel (1983)
Thalassoma hardwicke	Sixbar wrasse	Video of one individual at a single location	Aquarium	Big food pellet	Indo-Pacific	Pasko (2010)
Thalassoma jansenii	Jansen's wrasse	Video of multiple individuals at a single location	Lakshadweep Archipelago. India. Indian Ocean	Sea urchin	Indo-West Pacific	Jaishankar et al. (2024)
Thalassoma lunare	Moon wrasse	Video of one individual at a single location	Lakshadweep Archipelago. India. Indian Ocean	Sea urchin	Indo-Pacific	Jaishankar et al. (2024)
Thalassoma lunare	Moon wrasse	Description in a paper on anvil use	Aquarium	Big food pellet	Indo-Pacific	Pasko (2010)
Thalassoma lutescens	Yellow–brown wrasse	Description in a paper on another subject	Unknown	Unknown	Indo-Pacific	Heiser (1981)
Thalassoma pavo	Ornate wrasse	Description in a paper on another subject	Cabrera. Spain. Mediterranean Sea	Sea urchin	Eastern Atlantic, Mediterranean	Sala (1997)

Facebook. We encourage anyone to send us further observations via our website: https://fishtooluse.com.

To provide an overview of the phylogenetic distribution of anvil use in Fig. 1, we simplified the phylogeny of the Fish Tree of Life of Rabosky et al. (2018) with iTol and Inkscape and used FishBase (24 April 2024) to extract the number of Labridae species within each genus. We generated the map of anvil use observations in Fig. 3 with R software version 4.3.3 and the R packages ggplot2, ggrepel, maps. The map was then modified with Inkscape to include the distribution of New World *Halichoeres* species, extracted from FishBase in June 2024.

We conducted video analysis of the videos collected by the *Fish Tool Use* program. We scored the following for all anvil use events:

- Number of times the fish dropped its prey following impact against the anvil (presumably unintentional);
- Number of times the fish spat out its prey in between strikes. This differed from dropping the prey in that, when spitting, the fish still had the prey in its mouth after the strike, swam for a bit, stopped swimming, spat out the prey nearby, and retrieved it immediately (presumably intentional);
- Whether the wrasse struck the prey using the left side or right side of its body to investigate laterality of anvil use. A laterality index was calculated as (R – L) / (R + L), where R is the number of strikes using the right side of the body and L is the number of strikes using the left side. The index ranges from – 1 (extreme left-sidedness) to 1 (extreme right-sidedness). Individuals with an index below – 0.75 or above + 0.75 were considered lateralized with a clear preference for one side.
- Prey type from the video and/or by asking the observer (“Prey info source” in Table 2).
- Anvil type from the video and/or by asking the observer (“Anvil info source” in Table 2). Each anvil was classified into one of eight categories: rock, live coral, dead coral head, rubble, rock platform, gastropod shell, human-made object, or sand. A rock platform was defined as a solid and large surface forming the seafloor. A rock was defined as a distinct object with clear boundaries and excluded any human-made objects or items resembling coral, whether alive or dead. Rubble was defined as loose fragments of material, often from coral origin, that appear unanchored and scattered on the seafloor.
- Number of anvils used, presence or absence of a shell midden around the anvil, and shared characteristics among all anvils.
- Number of strikes and striking points. A fish may use multiple striking points on a single anvil.
- Duration of the anvil use event from the moment when the fish grabbed the prey item for the first time to the last successful strike that enabled the fish to eat the prey.
- Presence of and species of other fishes around the anvils at the time of the strike, and whether the tool-using wrasse chased these other fish. We considered the other fish to be predators of the tool-using wrasse if they were piscivorous fish and larger than it.

Finally, we analysed the video frame by frame to detect any differences in anvil use technique. We also estimated the life stages of the anvil-using wrasses in the videos based on their colour patterns. As it is the case with many wrasses, the five species in the present paper develop through successive life stages/colour phases: one juvenile colour phase, one adult initial colour phase, sometimes one or more intermediate phases, and one terminal colour phase (Roede 1972; Warner and Robertson 1978). It is possible to link some colour phases of *Halichoeres garnoti*, *H. poeyi*, and *H. brasiliensis* to a specific sex, but not for *H. bivittatus* where there are both males and females found in all colour phases (Roede 1972; Warner and Robertson 1978; Luis A. Rocha *personal communication*). We found no information relating to *H. radiatus* colour phases and sex in the literature. In addition to the videos we collected and analysed, we extracted information from several previous publications about wrasse tool use (such as the mean number of strikes per anvil use event) but we did not analyse the original video footage and only extracted information contained in the body of the text.

Results and discussion

Description of observations

A total of 19 observations of anvil use were collected in members of the New World *Halichoeres* clade. Seventeen were opportunistic observations in the wild, while the two other observations were induced, wherein sea urchins were offered as prey as part of research experiments. Three of the 19 observations came from the literature; Wainwright (1988) describes occurrences of anvil use in the wild and laboratory by several *Halichoeres bivittatus* and *H. garnoti* individuals; and Coyer (1995) describes one occurrence of anvil use in the wild by one *H. garnoti* individual (Tables 1, 2). The other 16 observations were from the *Fish Tool Use* community science program and included 13 videos and three written descriptions of anvil use: five videos for *H. bivittatus*; five videos and one description for *H. brasiliensis*; one video and one description for *H. garnoti* and *H. poeyi*; and one video for *H. radiatus* (Table 2).

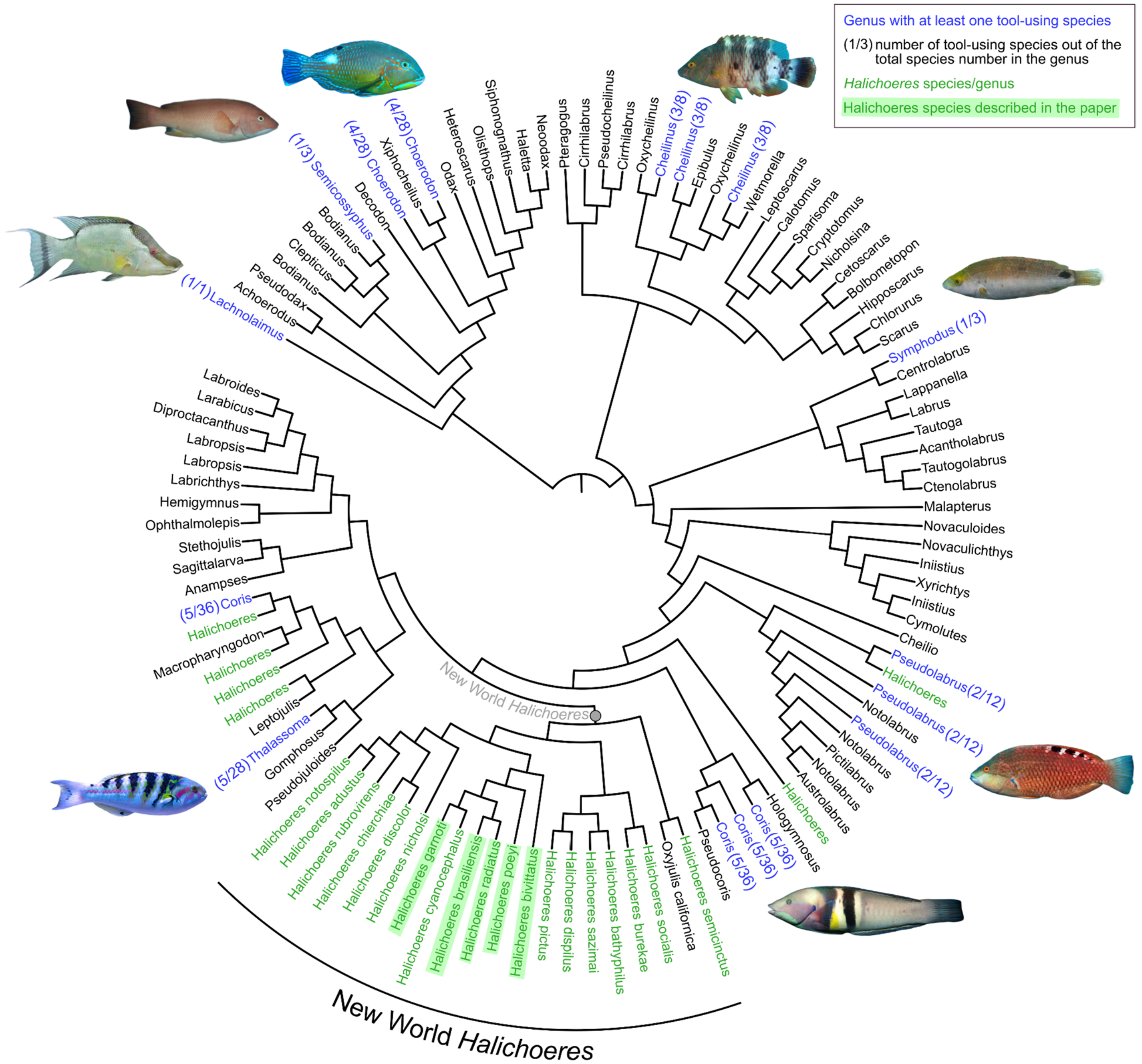

Fig. 1 Tool-using genera within the Labridae family. Labridae phylogeny has been simplified to the genus level except for the New World *Halichoeres,* for which species have been plotted. Some genera are polyphyletic and appear multiple times in the tree, such as *Choerodon*, *Cheilinus*, or *Coris*. Blue indicates a genus in which at least one species is known to use tools within the genus. The number of tool-using species out of the total number of species within the genus is indicated. Green indicates the *Halichoeres* genus, in which five of 82 species are known to use tools. The five New World Halichoeres species described in this paper are highlighted in green

Phylogenetic distribution of anvil use

The observations of anvil use involved five species in the New World *Halichoeres* clade: slippery dick (*H. bivittatus)*, Brazilian wrasse (*H. brasiliensis)*, yellowhead wrasse (*H. garnoti)*, blackear wrasse (*H. poeyi)*, and puddingwife wrasse (*H. radiatus*) (Figs. 1, 2, Table 2). These five species belong to the same sub-clade within the New World *Halichoeres,* along with *H. cyanocephalus* (Fig. 1). At the scale of the New World *Halichoeres*, the most parsimonious scenario is that anvil use appeared in the common ancestor of this specific sub-clade. But given how widespread anvil use is in the Labridae clade as a whole, it is more likely that the trait emerged at the base of the Labridae family rather than multiple independent evolutionary emergences of anvil use within the Labridae (Fig. 1). If this is the case, other Labridae species have either lost the anvil use ability or have not

Table 2 Description of observations of anvil use in New Word *Halichoeres* species

#obs	Species	Common name	Video name	Location	Date	Observer	Level of evidence
1	*Halichoeres bivittatus*	Slippery dick	Tool use by a slippery dick fish in South Caicos Island #1	Cockburn Harbour. Turks and Caicos Islands. West Atlantic Ocean	2022 Nov 09	C.E. O'Brien	Video of one individual at one location
2	*Halichoeres bivittatus*	Slippery dick	Tool use by a slippery dick fish in South Caicos Island #2	Cockburn Harbour. Turks and Caicos Islands. West Atlantic Ocean	2023 Mar 02	C.E. O'Brien	Video of one individual at one location
3	*Halichoeres bivittatus*	Slippery dick	Tool use by a slippery dick fish in South Caicos Island #3	Cockburn Harbour. Turks and Caicos Islands. West Atlantic Ocean	2023 Feb 26	C.E. O'Brien	Video of one individual at one location
4	*Halichoeres bivittatus*	Slippery dick	Tool use by a slippery dick fish in South Caicos Island #4	Cockburn Harbour. Turks and Caicos Islands. West Atlantic Ocean	2024 Feb 16	C.E. O'Brien	Video of one individual at one location
5	*Halichoeres bivittatus*	Slippery dick	Tool use by a slippery dick fish in South Caicos Island #5	Cockburn Harbour. Turks and Caicos Islands. West Atlantic Ocean	2020 Mar 08	C.E. O'Brien	Video of one individual at one location
6	*Halichoeres bivittatus*	Slippery dick	No video	Carrie Bow Cay. Belize. Caribbean Sea	1986–1987	Peter Wainwright	Description of multiple individuals at one location
7	*Halichoeres brasiliensis*	Brazilian wrasse	Tool use by a brazilian wrasse in Arraial do Cabo #1	Arraial do Cabo. Brazil. West Atlantic Ocean	2023 Mar 15	Jaqueline G. Toledo	Video of one individual at one location
8	*Halichoeres brasiliensis*	Brazilian wrasse	Tool use by a Brazilian wrasse in Santa Catarina #1	Arvoredo Island. Brazil. West Atlantic Ocean	2019 Oct 27	Thiago M. J. Fiuza	Video of one individual at one location
9	*Halichoeres brasiliensis*	Brazilian wrasse	Tool use by a Brazilian wrasse in Santa Catarina #2	Arvoredo Island. Brazil. West Atlantic Ocean	2019 Oct 27	Thiago M. J. Fiuza	Video of one individual at one location
10	*Halichoeres brasiliensis*	Brazilian wrasse	Tool use by a Brazilian wrasse in Trindade Island #1	Trindade. Brazil. West Atlantic Ocean	2018	Luisa Fagundes	Video of one individual at one location
11	*Halichoeres brasiliensis*	Brazilian wrasse	Tool use by a Brazilian wrasse in Trindade Island #2	Trindade. Brazil. West Atlantic Ocean	2018	Luisa Fagundes	Video of one individual at one location
12	*Halichoeres brasiliensis*	Brazilian wrasse	No video	Meros Island. Brazil. West Atlantic Ocean	1991–1996	Alfredo Carvalho-Filho	Description of multiple individuals at one location
13	*Halichoeres garnoti*	Yellowhead wrasse	Tool use by a yellowhead wrasse in South Caicos Island #1	Cockburn Harbour. Turks and Caicos Islands. West Atlantic Ocean	2023 Jun 10	C.E. O'Brien	Video of one individual at one location
14	*Halichoeres garnoti*	Yellowhead wrasse	No video	Natural National Park Tayrona. Colombia. Caribbean sea	2017–2023	Alejandra Puentes Sayo	Description of multiple individuals at one location
15	*Halichoeres garnoti*	Yellowhead wrasse	No video	Conch Reef. USA. West Atlantic Ocean	1994 Oct 22	Jim Coyer	Description of one individual at one location
16	*Halichoeres garnoti*	Yellowhead wrasse	No video	Carrie Bow Cay. Belize. Caribbean Sea	1986–1987	Peter Wainwright	Description of multiple individuals at one location

Table 2 (continued)

#obs	Species	Common name	Video name	Location	Date	Observer	Level of evidence
17	*Halichoeres poeyi*	Blackear wrasse	Tool use by a blackhear wrasse in Arraial do Cabo #1	Arraial do Cabo. Brazil. West Atlantic Ocean	2024 Apr 13	Carlos E. L. Ferreira	Video of one individual at one location
18	*Halichoeres poeyi*	Blackear wrasse	No video	Meros Island. Brazil. West Atlantic Ocean	1991–1996	Alfredo Carvalho-Filho	Description of multiple individuals at one location
19	*Halichoeres radiatus*	Puddingwife wrasse	Tool use by a puddingwife wrasse in Fernando de Noronha island #1	Fernando de Noronha island. Brazil. West Atlantic Ocean	2024 Mar 09	Mariana U. Goldschmidt	Video of one individual at one location

#obs	Species	Prey info source	Prey	Anvil info source	Anvil	Fish life stage info source	Fish life stage
1	*H. bivittatus*	Observer, video	Hermit crab	Observer, video	Rubble	Observer, video	Adult (Initial, intermediate or terminal phase)
2	*H. bivittatus*	Observer, video	Urchin	Observer, video	Rock platform, Rubble	Observer, video	Adult (Initial, intermediate or terminal phase)
3	*H. bivittatus*	Observer, video	Urchin	Observer, video	Rock platform, Rubble	Observer, video	Adult (Initial, intermediate or terminal phase)
4	*H. bivittatus*	Observer	Hermit crab	Observer, video	Rock platform, Rubble	Observer, video	Adult (Initial, intermediate or terminal phase)
5	*H. bivittatus*	Observer	Gastropod	Observer, video	Rock platform, Rubble	Observer, video	Adult (Initial, intermediate or terminal phase)
6	*H. bivittatus*	Observer	Crab	Observer	Rock	No info	no info
7	*H. brasiliensis*	Observer, video	Mollusc	Observer, video	Dead coral head, Unknown	Observer, video	Terminal phase
8	*H. brasiliensis*	Observer, video	Urchin	Video	Rock	Observer, video	Terminal phase
9	*H. brasiliensis*	Observer, video	Unknown	Video	Rock	Observer, video	Terminal phase
10	*H. brasiliensis*	Observer, video	Urchin	Video	Rock platform	Observer, video	Terminal phase
11	*H. brasiliensis*	Observer, video	Urchin	Video	Rock platform	Observer, video	Terminal phase
12	*H. brasiliensis*	Observer	Crab	Observer	Rock	No info	no info
13	*H. garnoti*	Observer, video	Brittle star	Observer, video	Gastropod shell, Rubble	Video	Third intermediate phase as described in Roede (1972)
14	*H. garnoti*	Observer	Mollusc	Observer	Rock, Rubble	Observer	Adult
15	*H. garnoti*	Observer	Scallop	Observer	Rock	Observer	Terminal phase
16	*H. garnoti*	Observer	Crab	Observer	Rock	No info	no info
17	*H. poeyi*	Observer, video	Mollusc	Observer, video	Rock	Video	Juvenile or initial phase
18	*H. poeyi*	Observer	Crab	Observer	Rock	Observer	Juvenile, initial and terminal phases
19	*H. radiatus*	Video	Crab	Video	Rock, Rock platform	Video	Initial phase

#obs	Species	Anvil use info source	Type	All anvil use captured	Duration event (s)	Successful anvil use	Preferred side to strike	Side striked	Laterality index	Other fish around anvils	Species of fish around	Tool-using-fish chasing other fish
1	*H. bivittatus*	Video	Wild	Left-censored and one gap in between	> 65	Yes	Both sides used	7R, 4L	0.27	Yes	Same species	Yes
2	*H. bivittatus*	Video	Wild	Left-censored	> 12	Yes	Both sides used	2R, 1L	0.33	Yes	Same species	No

Table 2 (continued)

#obs	Species	Anvil use info source	Type	All anvil use captured	Duration event (s)	Successful anvil use	Preferred side to strike	Side striked	Laterality index	Other fish around anvils	Species of fish around	Tool-using-fish chasing other fish
3	*H. bivittatus*	Video	Wild	Left-censored	> 14	Yes	Both sides used	2R, 6L	− 0.5	Yes	Same species	No
4	*H. bivittatus*	Video	Wild	Left-censored	> 87	Yes	Both sides used	5R, 2L	0.43	Yes	Same species, Thalassoma bifasciatum	Yes
5	*H. bivittatus*	Video	Wild	Left- and right-censored	> 172	No info	Both sides used	6R, 3R	0.33	Yes	Same species	Yes
6	*H. bivittatus*	Observer	Induced and Wild	no info	no info	Yes	No info	No info	No info	No info	–	No info
7	*H. brasiliensis*	Video	Wild	Left-censored	> 20	Yes	Both sides used	1R, 3L	− 0.5	No	–	No info
8	*H. brasiliensis*	Video	Wild	Left-censored	> 43	Yes	Both sides used	3R, 1L	0.5	No	–	No info
9	*H. brasiliensis*	Video	Wild	Left-censored	> 13	No, prey abandoned	Both sides used	1R, 1L	0	No	–	No info
10	*H. brasiliensis*	Video	Induced	Right-censored	Only one strike on video	No info	Only one strike on video	1R, 0L	Only one strike on video	Yes	Balistidae	No
11	*H. brasiliensis*	Video	Induced	Right-censored	> 23	No info	Both sides used	1R, 1L	0	Yes	Balistidae, Carangidae, Serranidae	No
12	*H. brasiliensis*	Observer	Wild	No info	No info	Yes	No info	No info	No info	No info	–	No info
13	*H. garnoti*	Video	Wild	Left-censored	> 80	Yes	Both sides used	5R, 3L	0.25	Yes	Halichoeres bivittatus, Lutjanidae, Pomacentridae, Thalassoma bifasciatum	No
14	*H. garnoti*	Observer	Wild	No info	No info	No info	No info	No info	No info	No info	–	No info
15	*H. garnoti*	Observer	Wild	Yes	> 180	Yes	Head left to right	0R, 6L	− 1	Yes	Same species	No info

Table 2 (continued)

#obs	Species	Anvil use info source	Type	All anvil use captured	Duration event (s)	Successful anvil use	Preferred side to strike	Side striked	Laterality index	Other fish around anvils	Species of fish around	Tool-using-fish chasing other fish
16	*H. garnoti*	Observer	Induced and Wild	No info	No info	Yes	No info	No info	No info	No info	–	No info
17	*H. poeyi*	Video	Wild	Left- and right-censored	> 27	No info	Both sides used	4R, 3L	0.14	Yes	Pomacanthidae, Same species, Serranidae	Yes
18	*H. poeyi*	Observer	Wild	No info	No info	Yes	No info	No info	No info	Yes	Same species	No info
19	*H. radiatus*	Video	Wild	Left- and right-censored	> 14	No info	Both sides used	2R, 4L	− 0.33	Yes	Acanthuridae, Pomacentridae, Same species, Thalassoma noronhanum	No

#obs	Species	Nb of times prey dropped	Nb of times prey spit	Nb anvils	Nb of strikes	Striking points	Nb anvil changes	Nb anvil stays	Nb anvil changes with fish around	Nb anvil stays with fish around
1	*H. bivittatus*	3	4	≥ 3	≥ 11	(1) 1SP-3S 2SP-5S 3SP-1S; (2) 1SP-1S; (3) 1SP-1S	3	7	3	7
2	*H. bivittatus*	0	0	≥ 2	≥ 3	(1) 1SP-2S; (2) 1SP-1S	1	1	0	0
3	*H. bivittatus*	3	3	≥ 7	≥ 8	(1) 1SP-1S; (2) 1SP-1S; (3) 1SP-1S; (4) 1SP-1S; (5) 1SP-1S 2SP-1S; (6) 1SP-1S; (7) 1SP-1S	6	1	5	1
4	*H. bivittatus*	1	3	≥ 6	≥ 7	(1) 1SP-1S; (2) 1SP-1S; (3) 1SP-1S; (4) 1SP-1S; (5) 1SP-2S; (6) 1SP-1S	5	1	4	0
5	*H. bivittatus*	1	1	≥ 3	≥ 9	(1) 1SP-1S; (2) 1SP-4S; (3) 1SP-3S	2	6	2	6

Table 2 (continued)

#obs	Species	Nb of times prey dropped	Nb of times prey spit	Nb anvils	Nb of strikes	Striking points	Nb anvil changes	Nb anvil stays	Nb anvil changes with fish around	Nb anvil stays with fish around
6	*H. bivittatus*	No info	No info	No info	No info	No info	No info	No info	No info	No info
7	*H. brasiliensis*	2	0	≥2	≥4	(1) unknown; (2) 1SP-2S	1	2	0	0
8	*H. brasiliensis*	1	2	≥3	≥4	(1) 1SP-1S; (2) 1SP-1S; (3) 1SP-1S 2SP-1S	3	1	0	0
9	*H. brasiliensis*	0	2	≥2	≥2	(1) 1SP-1S; (2) 1SP-1S	1	0	0	0
10	*H. brasiliensis*	Only one strike on video	Only one strike on video	Only one strike on video	Only one strike on video	Only one strike on video	Only one strike on video	Only one strike on video	Only one strike on video	Only one strike on video
11	*H. brasiliensis*	1	0	≥1	≥3	(1) 1SP-1S 2SP-1S 3SP-1S	0	3	1	2
12	*H. brasiliensis*	No info	No info	No info	No info	No info	No info	No info	No info	No info
13	*H. garnoti*	3	4	≥7	≥8	(1) 1SP-1S; (2) 1SP-1S; (3) 1SP-1S; (4) 1SP-1S; (5) 1SP-1S; (6) 1SP-1S 2SP-1S; (7) 1SP-1S	6	1	4	1
14	*H. garnoti*	No info	No info	No info	No info	No info	No info	No info	No info	No info
15	*H. garnoti*	No info	No info	1	6	No info	0	5	0	5
16	*H. garnoti*	No info	No info	No info	No info	No info	No info	No info	No info	No info
17	*H. poeyi*	0	4	≥1	≥7	(1) 1SP-7S	0	6	0	6
18	*H. poeyi*	No info	No info	No info	No info	No info	No info	No info	No info	No info
19	*H. radiatus*	3	1	≥2	≥6	(1) 1SP-1S 2SP-1S 3SP-1S; (2) 1SP-2S; (1) 4SP-1S	2	3	2	3

Observations are from the literature and the *Fish Tool Use* community science program. The columns labelled 'info source' provide the sources of information for the prey, anvil, fish life stage, and description of anvil use (the description ranges from the columns 'Type' to 'Nb anvil stays with fish around'). Column 'Type': (i) 'Wild': the fish found the prey by itself; (ii) 'Induced': a prey item was provided by a human observer. Column 'All anvil use captured': (i) 'Yes': all of the anvil use event was captured on video; (ii) 'Left-censored': the video started after the beginning of anvil use—the video is possibly missing the first strikes; (iii) 'Right-censored': the video ended before the end of anvil use—the video is possibly missing the last strikes. Column 'Side striked': R indicates the number of strikes in which the fish used the right side of its body to strike the prey and L is the number of strikes using the left side. Column 'Striking points': the number of anvils, the number of different striking points on an anvil and the number of strikes on a striking point. For example, '(1) 1SP-2S; (2) 1SP-1S 2SP-1S' indicates that for the first anvil (1) there were only one striking point 1SP on which the wrasse had two strikes 2S, then for the second anvil (2) the wrasse visited, they had one striking point 1SP with one strike 1S and a second striking point 2SP on which the wrasse again had one strike 1S yet been observed doing it. More study will likely discover many other wrasse species using anvils.

Geographic distribution of anvil use

All observations of anvil use by *H. bivittatus* were made near a research station in the Turks and Caicos Islands. For *H. brasiliensis,* observations were made at four different locations in Southern Brazil, including Trindade Island situated > 1,000 km away from the southeastern coast of Brazil. For *H. garnoti*, one video was filmed at the same research station in the Turks and Caicos Islands as *H. bivittatus,* and one description came from a coastal marine park in Colombia. Finally, there are two observations of *H. poeyi* from Southern Brazil (Fig. 3) and one observation of *H. radiatus* at Fernando de Noronha Island located ~ 350 km away from the northeast coast of Brazil.

All of the locations described above are new locations where anvil use has not been previously described (Fig. 3). They extend the known geographic range of fish anvil use to the southern part of the Caribbean, the tropical Western Atlantic and the temperate South-west Atlantic, both for the New World *Halichoeres* clade and for Labridae in general.

Combined with previous observations, anvil use in New World *Halichoeres* is widely distributed across the Caribbean and Western Atlantic Ocean. The current southern limit of this behaviour is Southern Brazil, the northern limit is the Florida Keys, the eastern limit is Trindade Island and the western limit is Belize. This encompasses almost the entire distribution of the New World *Halichoeres* species (purple on Fig. 3) outside of the Eastern Pacific Ocean.

Anvil use technique and laterality

In all observations across all species, anvil use technique was similar and involved a quick lateral movement. The fish swam to orient itself in relation to the hard surface (anvil) while holding the prey item in its mouth, curved its body away from the anvil either to the right or the left, and then rapidly swung its body in the other direction to strike the prey item on the anvil (Fig. 4). Wrasses often spat out the prey between strikes and retrieved it immediately after, likely to adjust its grip on the prey item (spitting prey was observed in nine of the 19 observations, not observed in three observations, and not recorded or otherwise unknown for six observations; Table 2 column 'Nb of times prey spit').

Interestingly, wrasses do not seem to favour a particular side of their body when using anvils. They used both sides of their body equally to break open their prey in all video observations, curving their body either to the right or left before the strike (Table 2 column 'Preferred side to strike'). Individuals were not lateralized (laterality index in between − 0.75 and 0.75 for all anvil use events in Table 2 column 'Laterality index'). One exception is Coyer's (1995) description, in which the wrasse was reported as only striking prey on one side of its body, but without video evidence, it is not possible to verify this. The overall absence of laterality in New World *Halichoeres* tool use was unexpected since tool use is strongly lateralized in primates and New Caledonian crows (Rutledge and Hunt 2004) and laterality is common in fish of various species across a wide range of contexts such as escape response, feeding and navigation (Bisazza and Brown 2011). Laterality has been hypothesised as a neuromorphological solution for increasing the efficiency of complex motor tasks (Rutledge and Hunt 2004). It is possible that the efficiency advantage of lateralisation may be exceeded by the advantage a fish

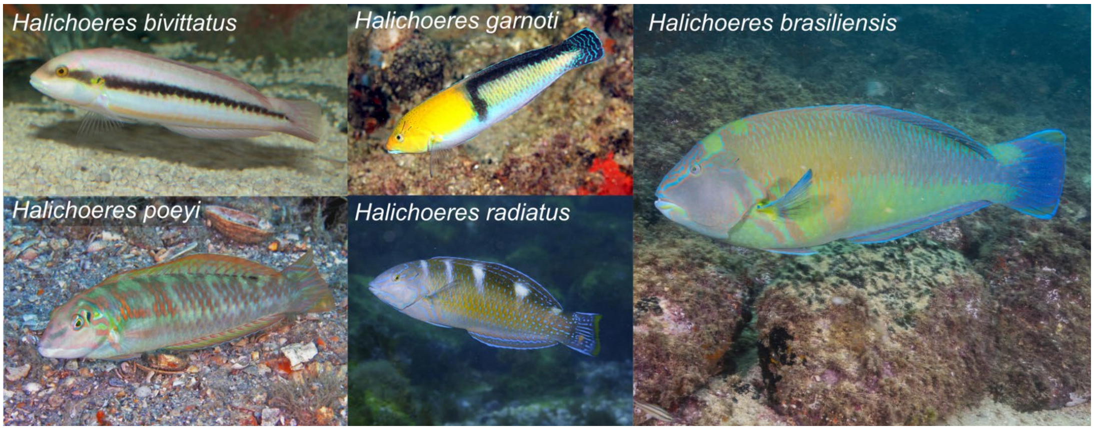

Fig. 2 Pictures of the five New World *Halichoeres* species observed using rocks as anvils while foraging. The *Halichoeres bivitattus* and *H. radiatus* are shown in the intermediate colour phase. All of the other fish are in their terminal phase colour. Pictures by Brian Gratwicke, Kevin Bryant and João Paulo Krajewski

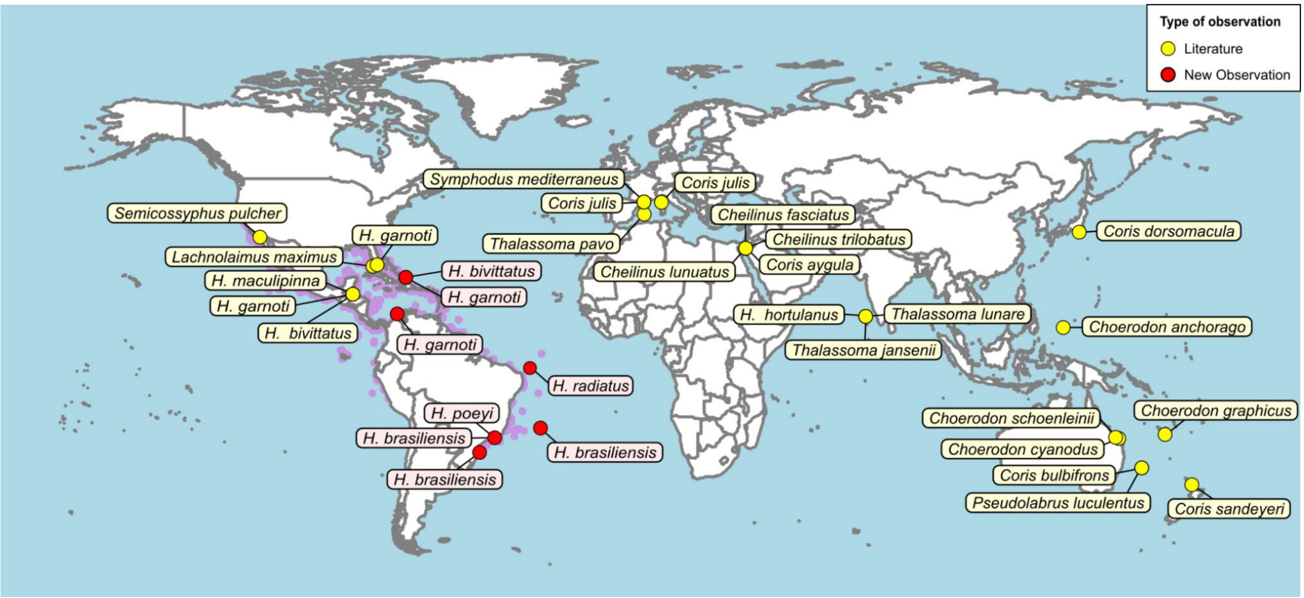

Fig. 3 Locations of anvil use observations in Labridae (wrasses). Observations from existing literature are noted in yellow and new observations from the *Fish Tool Use* program are in red. The distribution of the New World *Halichoeres* species is marked in purple. The New World *Halichoeres* species are *H. bivittatus, H. brasiliensis, H. garnoti*, *H. poeyi*, and *H. radiatus*; *H. maculipinna* is not part of the New World *Halichoeres*

gains from the flexibility of using anvils whatever their orientation, which would explain why fish anvil use is not lateralised.

Anvil selection

Wrasses were very flexible in their selection of anvils. They used a wide variety of hard surfaces in their environment to crack open their prey, including rocks, the edges of rock platforms, and rubble of diverse origin (Table 2 column ‘Anvil’). One wrasse even used a live conch shell (*Aliger gigas*) as an anvil in observation #13. Flexibility in anvil selection has also been observed in *Thalassoma jansenii*, *H. hortulanus*, and *Choerodon graphicus* which have used rocks, rock platforms, rubble, dead and live corals, human-made objects, and shells as anvils (Pryor 2020; Jaishankar et al. 2024).

We did not see any obvious characteristics shared by anvils (apart from the fact that they were hard and sufficiently encrusted not to move). There were no noticeable middens of broken shells around anvils that could indicate an object had been used repeatedly as an anvil. Wrasses regularly changed anvils over the course of a single video, using multiple anvils to crack open their prey in 11 out of

Fig. 4 Sequence of actions during an anvil use event. A yellowhead wrasse, *Halichoeres garnoti*, striking a brittle star arm on rubble by swinging its head from the left to the right. Screenshots from video observation #13

14 observations (Table 2 column ‘Nb of anvils’). Between strikes, wrasses changed anvils 53% of the time (average ratio ‘Nb of anvil changes’/(‘Nb of anvil changes’ + Nb of anvil stays’) in Table 2) and used the same anvil 47% of the time. Many anvil changes during anvil use events have also been observed in *H. hortulanus* (multiple anvils used in all 12 observations reported by Jaishankar et al. 2024) and *C. graphicus* (multiple anvils used in two out of three observations in Pryor and Milton 2019, two out of four observations in Pryor and Milton 2023).

Wrasses in the present study typically used multiple striking points on an anvil. Interestingly, they generally used a striking point only once, either changing to a different striking point on the same anvil or changing anvils – Forty of the striking points in Table 2 were used for a single strike while only nine of the striking points were used for multiple strikes (Table 2 column ‘Striking points’ noting the prevalence of ‘1S’ which indicates a single strike on the striking point). The most extreme example of this is video observation #1 at 00:42 in which a *H. bivittatus* wrasse struck its prey on three different striking points belonging to two different anvils over the course of 4 s, one of them being on a new anvil. This again might be explained by how opportunistic and flexible wrasses are in their tool selection, exploiting any potential hard surface. They might also do this to strike the prey at multiple points, since some parts of the prey may be easier to break open.

Anvil use costs and benefits

Anvil use is likely costly to wrasses. Estimating these costs would require calculating the number of strikes, the duration and the probability of a successful anvil use event (i.e., resulting in the wrasse eating the prey item) and the probability of an unsuccessful anvil use event. However, we are unable to estimate the probability of successful/unsuccessful events with so few observations. There was only one instance of an unsuccessful tool use event in our dataset in which the wrasse abandoned the prey for an unknown reason (Table 2 column ‘Successful tool use’). In addition, most observations were censored, meaning that the video did not capture the whole anvil use event, so we are underestimating the number of strikes and duration. Keeping these limitations in mind, we found that successful anvil use events required an average of ≥ 6 strikes (min ≥ 2, max ≥ 11) and lasted on average ≥ 1 min (min ≥ 12 s, max ≥ 3 min). The multiple strikes involved in a successful anvil use event corroborates other observations in *H. hortulanus*, *T. jansenii*, and *C. graphicus* (Jaishankar et al. 2024; mean ≥ 14 strikes in Pryor and Milton 2019; mean ≥ 11 strikes in Pryor 2020; mean = 3 strikes in Pryor and Milton 2023). Strikes are likely to be energetically costly as the lateral movement involved is rapid and vigorous, and indeed, powerful enough to push the wrasse away from the anvil after a strike and to cause the wrasse to frequently lose hold of the prey item (in nine out of 19 observations; three observations in which prey was not dropped, and seven observations in which it is unknown whether the prey item was dropped; Table 2 column ‘Nb of times prey dropped’).

Other costs of anvil use arise from the presence of other animals which may act as scavengers of the wrasses’ prey or predators of the anvil-using wrasse. The presence of scavengers likely increases the costs of anvil use through the energy expenditure associated with chasing and being chased by the scavengers and decreases the benefits through the loss of the prey item or part of the prey item. There were fish around the anvil-using wrasse in 12 observations (no fish around in three observations, and whether other fish were present is unknown for four observations; Table 2 column ‘Other fish around’). Among those 12 observations, there were four observations in which the anvil-using wrasse was actively chasing wrasses of the same species (Table 2 column ‘Fish chasing other fish’). In observation #13, a juvenile slippery dick stole a brittle star arm from a yellowhead wrasse that had just broken it off using a rock. This finding accords with another study in which the anvil-using wrasse *C. graphicus* was observed with fish in its vicinity during anvil use in 15 of 16 observations (Pryor and Milton 2021). Among these 15 observations, anvil-using wrasses chased other fish during three observations and part of its prey item was stolen in two observations. However, the presence of fish around the anvil did not necessarily force the anvil-user to move to another anvil. On average, 85% of anvil changes occurred with fish around and 85% of stays at the same anvil occurred with fish around (Table 2 columns ‘Nb anvil changes with fish around’ and ‘Nb anvil stays with fish around’). Finally, anvil use might put wrasses at greater risk of predation as they are focused on their prey item and actions, and predators might be attracted by the noise generated from banging the prey and the motion of the wrasse and scavengers. However, we did not observe predators in the vicinity of the anvil-user wrasses in any observation. Predators may not take advantage of anvil use to increase their predation rate or predators may have been deterred by the presence of human observers.

Anvil use must have substantial benefits to off-set these costs. The benefits likely arise from accessing prey that would otherwise be inaccessible. Wrasses used anvils to break open a wide diversity of hard-shelled prey: crabs, sea urchins, shelled molluscs, hermit crabs, and a brittle star (Table 2 column ‘Prey’). In the literature, wrasses have been recorded using anvils to break open these prey types as well as a juvenile sea turtle, an isopod and large food pellets (Table 1 column ‘Prey’). Interestingly, wrasses also use anvils to split large prey into smaller pieces that the wrasse can ingest, as in observation #13 (Table 1), in which a wrasse continues to strike the brittle star arm even after it has already broken off the brittle star body. Wrasses successfully broke their prey item in 12 of the 19 observations reported here and abandoned it in only one observation for unknown reasons (success was unknown in six observations; Table 2 column 'Successful.tool.use'). A high success rate for anvil use has also been previously observed in *C. graphicus* (three successful anvil use events out of three events in Pryor and Milton 2019, 4 out of 4 in Pryor and Milton 2023).

The benefits of accessing a greater range of prey may be particularly important for small wrasses that are limited by gape size and the pressure they can exert with their pharyngeal teeth to break open prey without an anvil. Using tools likely open up novel foraging niches that provide high value prey. However, the wrasses using anvils reported here were adult phases (initial, intermediate, or terminal phases) in 14 of the 16 observations in which it was possible to determine the wrasse colour phase (Table 2 column 'Fish life stage'). These observations should not necessarily be taken to mean that anvil use is more common in adult life stages than juvenile stages. The behaviour of larger adult wrasses may be more readily observed than that of juvenile wrasses if larger wrasses' behaviour attracts more human attention or if larger wrasses are less cautious around humans. More observations are needed to confirm if anvil use is largely limited to adult life stages in wrasse. If confirmed, this link could be due to the limited strength and/or size of smaller wrasses' jaws, which might not have the necessary grasping strength to be able to move the prey rapidly through the water for several centimetres before hitting it on a hard surface.

Conclusions

The present study described new observations of anvil use in the New World *Halichoeres* clade which extend the known geographical and taxonomic range of this behaviour in wrasses. Anvil use seems to be a versatile skill used in many locations around the world by numerous Labridae to crack open a wide array of hard-shelled prey on multiple surfaces, even during the course of a single anvil use event. Anvil use is likely more common among wrasses than currently recorded, and we encourage further in situ observations to fully document the geographic and taxonomic extent of this behaviour. Systematic experiments in which prey is offered to wrasse could achieve this more efficiently than opportunistic observations, especially in species that live in an environment with little hard-shelled prey available. This technique has already been successful in triggering instances of anvil use (Table 2; Jaishankar 2024). We also encourage people to contribute to our *Fish Tool Use* community science program (https://fishtooluse.com). More observations will shed light on the evolution of anvil use behaviour in wrasses and provide insights into its development, costs, and benefits.

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Author contributions Juliette Tariel-Adam and Culum Brown contributed to the study design and funding acquisition. Jaqueline G. Toledo, C. E. O'Brien, and Sergio R. Floeter acquired the data. J.T-A contributed to the data curation, analysis and visualisation, and drafted the manuscript. All authors critically revised it.

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Data availability All video observations are available at https://www.youtube.com/playlist?list=PLEGR7FN3Lr-54JaQ3gURVCkGsvQ_mXwkH. The two R scripts used to build the tables and the map are available on GitHub at https://github.com/JulietteTarielAdam/Tool-use-by-New-World-Halichoeres.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval The community science program *Fish Tool use* received human ethic approval by The Faculty Ethics Subcommittees at Macquarie University which operates in accordance with the National Statement on Ethical Conduct in Human Research 2007 (updated July 2018). This study was thus performed in line with the principles of the 1964 Helsinki Declaration. All participants gave their consent to the authors to analyse and share their videos alongside their name.

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