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Biology of Tropical Birds

Hover-gleaning decapods from floating sargassum: a novel foraging behavior by Great-tailed Grackle (*Quiscalus mexicanus*) on Isla Cozumel

Captura de decápodos sobre sargazo flotante mediante vuelo estacionario: un comportamiento de forrajeo novedoso de *Quiscalus mexicanus* en la isla de Cozumel

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ABSTRACT. The Great-tailed Grackle (*Quiscalus mexicanus*) is widely recognized as a terrestrial, diet-generalist species, yet its use of over-water foraging remains poorly documented. Here, I describe a novel over-water foraging strategy used by Great-tailed Grackles on Isla Cozumel, Mexico. Over 13 hours of observation across 12 days between 24 July and 21 August 2022, I observed brown-plumaged (presumed female) grackles using a consistent sequence of flight modalities to hover-glean sargassum swimming crabs (*Portunus sayi*) from floating rafts of macroalgae. I recorded 57 foraging excursions when floating sargassum was present, with a median distance from shore of 44 m and a median duration of 10 s. The capture success rate was 60%. An energetic model indicates this strategy is plausible, with an estimated net energy gain of 244–771 J from an average-sized crab (18 mm carapace width) after 22 s of total effort by a female grackle (130 g). This behavior likely emerged in the western Caribbean following the onset of recurring sargassum inundations in 2014 to 2015 and serves as an example of one species' response to recent environmental change.

RESUMEN. *Quiscalus mexicanus* es una especie ampliamente reconocida por presentar hábitos terrestres y dieta generalista, aunque el uso de estrategias de forrajeo sobre el agua ha sido escasamente documentado. En este trabajo describo una estrategia novedosa de forrajeo sobre el agua utilizada por *Q. mexicanus* en la isla de Cozumel, México. Durante más de 13 horas de observación a lo largo de 12 días, entre el 24 de julio y el 21 de agosto de 2022, observé individuos de plumaje pardo (presumiblemente hembras) empleando una secuencia consistente de modalidades de vuelo para capturar, mediante vuelo estacionario y recolección sobre superficies, cangrejos nadadores del sargazo (*Portunus sayi*) presentes en balsas flotantes de macroalgas. Registré 57 incursiones de forrajeo cuando había sargazo flotante, con una distancia mediana a la costa de 44 m y una duración mediana de 10 s. La tasa de éxito de captura fue del 60 %. Un modelo energético indica que esta estrategia es viable, con una ganancia energética neta estimada de entre 244 y 771 J a partir de un cangrejo de tamaño promedio (18 mm de ancho del caparazón), tras un esfuerzo total de 22 s por parte de una hembra de *Q. mexicanus* de 130 g. Este comportamiento probablemente surgió en el Caribe occidental tras el inicio de los recurrentes arribazones de sargazo entre 2014 y 2015, y constituye un ejemplo de la respuesta de una especie a los cambios ambientales recientes.

Key Words: *adaptation; behavioral flexibility; Caribbean; energy; foraging; Great-tailed Grackle; hover-gleaning; sargassum*

INTRODUCTION

Recent recurrent sargassum inundations have altered coastal habitats across the western Caribbean. Here I describe previously undocumented behavior in which brown-plumaged Great-tailed Grackles on Isla Cozumel forage for decapods from floating sargassum, and I quantify the plausibility of this novel behavior using energetic modeling.

Great-tailed Grackle diet and foraging

The Great-tailed Grackle (*Quiscalus mexicanus*) is widely known for its varied diet and foraging techniques. As a member of the New World blackbirds (family Icteridae, which includes blackbirds, bobolinks, grackles, meadowlarks, and orioles), the Great-tailed Grackle is a large, sexually dimorphic passerine and year-round resident of Central America, northern South America, and southern portions of central and western North America. It tends to inhabit open areas near water and wetlands, and secondary forests in tropical and subtropical zones (Johnson and Peer 2022). Great-tailed Grackles are also well-adapted to urban and human-modified environments, including agricultural fields, plantations, pastures, and feedlots (e.g., Skutch 1954, Johnson and Peer 2022). The Great-tailed Grackle is an omnivorous forager that uses its bill to capture diverse food types, including insects and larvae, grains, seeds, fruits, berries, and other plant material, small crustaceans, and worms (Skutch 1954). They are also known to frequent landfills and parking lots, farm fields, and livestock feedlots (e.g., Rappole et al. 1989, Bush 2005, Bodenchuk and Bergman 2020).

Range expansion and behavioral flexibility

Evidence of the Great-tailed Grackle's adaptability also comes from its considerable range expansion. Early records suggest the Great-tailed Grackle originated from the tropical lowlands of eastern Mexico before introduction to the Aztec capital of Mexico City during the late 15th century (Haemig 2012). A stable breeding population of Great-tailed Grackles that was present in southern Texas by the 1880s expanded northward to the Minnesota–North Dakota border by 1995 (Dinsmore and Dinsmore 1993, Wehtje 2003). In addition to the rapid spread of human-modified environments, the social behavior, omnivorous diet, habitat preferences, adaptability, and long association of grackles with human settlements likely contributed to their expansion (Wehtje 2003).

Numerous laboratory and field studies (e.g., Logan 2016, Logan et all 2023, 2025, Breen and Deffner 2024) have linked the rapid range expansion of the Great-tailed Grackle with its behavioral

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flexibility, which is defined as the ability to modify behavior in the face of changing circumstances (Mikhalevich et al. 2017). Although this study is not about behavioral flexibility, it draws on this literature as a background for why novel foraging behaviors are not unexpected in this species. In comparison with studies of range expansion that emphasize flexibility across geography, this study offers an opportunity to examine adaptability within an established geographic range.

Sargassum habitat

With the sudden appearance of sargassum in the western Caribbean more than a decade ago, coastal habitats of the Great-tailed Grackle have experienced substantial environmental change. Originally confined to the Sargasso Sea, large masses of *Sargassum* spp., a holopelagic macroalga, first appeared in the Great Atlantic Sargassum Belt in 2011 and have become an annual occurrence along the shores of West Africa, the Caribbean, and the Gulf of Mexico (e.g., Wang et al. 2019, Jouanno et al. 2025, Lapointe et al. 2025).

On the open ocean, floating mats of sargassum provide important habitat for diverse endemic and non-endemic taxa, including sessile and motile invertebrates and fish species (e.g., Martin et al. 2021, van Tussenbroek et al. 2024a, 2024b). Numerous seabirds also forage in association with this important ecosystem (Moser and Lee 2012). Guided by wind, ocean currents, and bottom geometry, approaching masses of sargassum introduce new species and nutrients to coastal environments (e.g., McGillicuddy et al. 2023, van Tussenbroek et al. 2024a). The decay of beach-cast sargassum is associated with numerous environmental, economic, and health impacts (e.g., van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2025).

Here I document Great-tailed Grackles gleaning crabs from floating sargassum along the west coast of Cozumel Island. This behavior is notable given that grackles are typically terrestrial ground foragers and that the sargassum habitat appeared only recently in the western Caribbean. The aims of this study are to (1) describe the novel foraging strategy, (2) summarize basic metrics of this behavior, and (3) evaluate the energetic plausibility using a simple model.

METHODS

This study is based on 13 hours of observation across 12 days between 24 July and 21 August 2022 on Isla Cozumel, Mexico (Appendix 1). I used opportunistic observations from a single vantage point (ocean-facing balcony), therefore my observations of foraging activities were limited to a 150 m radius. Located on the lee side of the island relative to the prevailing easterly wind, the study site (20°32'11.4" N, 86°56'16.4" W) is situated within a narrow coastal strip of residential properties bordered by inland low tropical forest and tropical semi-deciduous forest. Great-tailed Grackles are common residents on the island, with two to five individuals typically observed per 10 min window at the site, where they forage among the palm trees, sand, structures, and lawns throughout the day.

Observations and data

For this study, I documented grackle behavior whenever sargassum was present and grackles exhibited foraging activity during the study period. Observation sessions lasted 10 to 70 min in duration between 7:30 AM and 7:30 PM local time (Appendix 1) and utilized binoculars (10 x 32) and still photographs. I used the locations of fixed buoy lines and bathymetric features to estimate distances (±10–20%) from shore using Google Earth images. I estimated flight duration by manual counts approximating seconds (± 5%–10%). When possible, I used photo metadata to supplement the manual time estimates. For each foraging event, I recorded the time, duration, number of individuals, sex, maximum distance from shore, foraging success, and type of prey captured. General information about the weather conditions and sargassum distribution were also noted. I used Microsoft Excel and SPSS for data analysis, modeling, and for preparing illustrations.

Models of energy costs and benefits

Here I describe the structure, methods, and key assumptions used to develop a simple model for evaluating the energetic plausibility of over-water foraging for crabs. Additional information, including a table of parameters, sensitivity bounds, and derivations, is in Appendix 1. I estimated the sizes of the foraged crabs from photos by comparing with the length of the grackle's bill (assumed to average 22 mm; Johnson and Peer 2022). Next, I calculated the wet mass of the crab from the carapace width using a power-law relationship developed using paired data from sargassum swimming crabs from West and Randy Brooks (2018) and from V. Monroy Velazquez (*personal communication*). I then used the mass data to estimate the energy density of tissue and shell in sargassum swimming crabs using nutrition information from a blue crab proximate (USDA 2024, Fuso et al. 2025) and the digestibility of tissue and shell by passerines, poultry, and seabirds (Potter et al. 1962, Twedt 1985, Jackson et al. 1992, Barrett et al. 2007). For the energetic costs of foraging, I assumed an average foraging time to success of 21.5 s (this study), an average mass of 130 g for female Great-tailed Grackles (Johnson and Peer 2022), and a basal metabolic rate (BMR) of 0.9 W (Lasiewski and Dawson 1967, McKechnie and Wolf 2004). Using data from passerine scaling studies (Bishop 1999, Ward et al. 2001), I estimated the energetic cost of forward flight and hovering to average 13 times the basal metabolic rate.

RESULTS

I observed 57 foraging excursions, averaging 2–13 per hour when floating sargassum was present (Appendix 1). In most cases (> 95%), a brown-plumaged Great-tailed Grackle foraged alone, but I also observed loose foraging groups of up to four individuals. Observations of eye color and plumage characteristics suggest that most of the foraging individuals were mature female grackles. On rare occasions, one or more brown-plumaged (presumed female) grackles were joined by a male on their flight over the ocean, but I never observed a male grackle engaging in active foraging.

Behavior sequence of foraging events

Successful foraging excursions by Great-tailed Grackles over floating sargassum always exhibit five phases. The outbound phase begins when a Great-tailed Grackle leaves a shoreline perch and flies directly toward rafts of sargassum, typically distributed in irregular and elongate masses subparallel to shore (Fig. 1a). During the searching phase, grackles generally assume a more vertical posture as they fly slow and low over the water (Fig. 1b); brief periods of intervening flight with more typical in-flight body posture occur between rafts. Once a grackle identifies potential

Fig. 1. Photographs illustrating the study site and Great-tailed Grackle (*Quiscalus mexicanus*) foraging behavior. (A) Floating mats of Sargassum spp. on 24 July 2022. The line of white buoys marking the innermost sargassum rafts is subparallel to shore and 34 m distance; the most distant sargassum rafts are ~200 m from shore. (B) A brown-plumaged Great-tailed Grackle hovering over a sargassum raft at ~36 m from shore on 25 July 2022. (C) A Great-tailed Grackle hover-gleaning from floating sargassum at ~37 m from shore on 31 July 2022. Note, the bird's toes are touching floating sargassum while hovering and gleaning. (D) A brown-plumaged Great-tailed Grackle preparing to eat a crab after a successful foraging excursion out to ~85 m from shore on 24 July 2022.

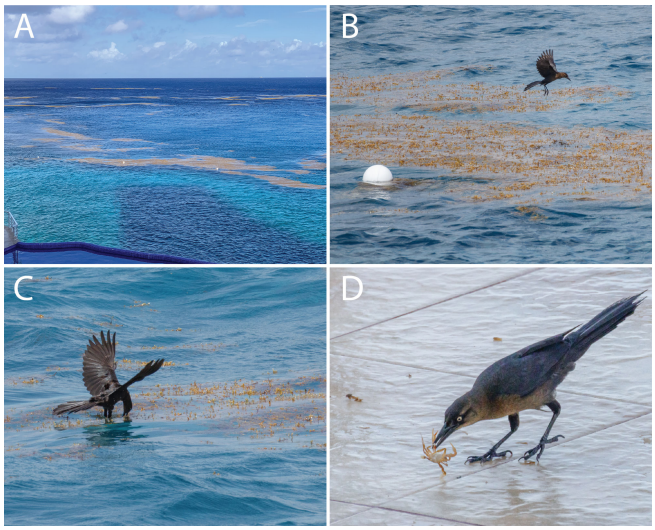
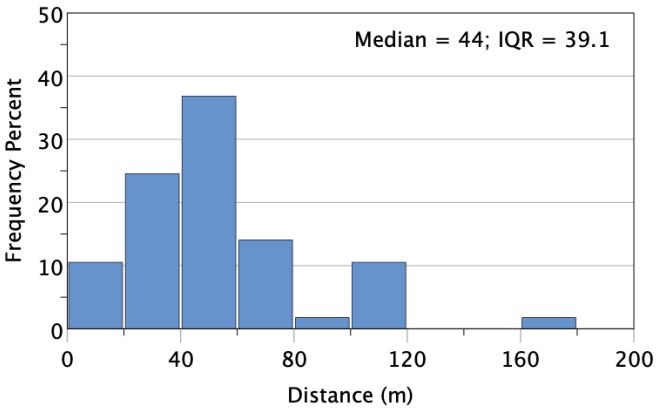


Fig. 2. Histogram of foraging distances (n = 57).



prey, it momentarily hovers in place (hovering phase), then lowers itself to the surface of the floating sargassum to capture and control the prey (gleaning phase) with its bill (Fig. 1c), before flying back to shore (inbound phase) and consuming the prey (Fig. 1d). It is not uncommon for a bird to cycle through several searching and hovering phases within a single foraging excursion. Because floating sargassum appears to provide insufficient buoyancy, grackles flap their wings as their toes touch the macroalgae. These regularly sequenced behaviors suggest consistent foraging strategies rather than opportunistic chance.

Spatial and temporal characteristics of foraging

Although Great-tailed Grackles forage over floating sargassum up to 180 m from shore, the median distance was 44 m, and < 15% of forages occurred at distances > 80 m from shore (Fig. 2). Foraging events ranged in duration from four to 58 s, with a median of 10 seconds; less than 10 percent of forages were > 30 seconds in duration (Fig. 3). These brief, moderate-distance excursions suggest that over-water foraging is beneficial when prey is accessible and sufficiently distributed.

Foraging success and prey composition

Of the 57 foraging events that I observed, a grackle returned to shore with prey 39 times, for an average prey capture rate of 59.7% and an average foraging time per success of 21.5 s. Upon reaching shore, most inbound Great-tailed Grackles flew to a level surface (e.g., tiled deck, walkway, masonry wall, sand, or grass), where they processed captured crabs by shaking and rubbing them on the ground before consumption; subsequent video observations also indicate that grackles occasionally use their feet to control crabs during processing. In 30 of the 39 successful forages that I observed, I identified the captured prey as sargassum swimming crab (*Portunus sayi*) from photographs (e.g., Fig. 1D) and from recovered body parts. I could not identify the remaining nine captured prey from binocular observations or photographs. In summary, the over-water foraging strategy exhibited by brown-plumaged (presumed female) grackles appears to be successful for targeting a specific type of prey.

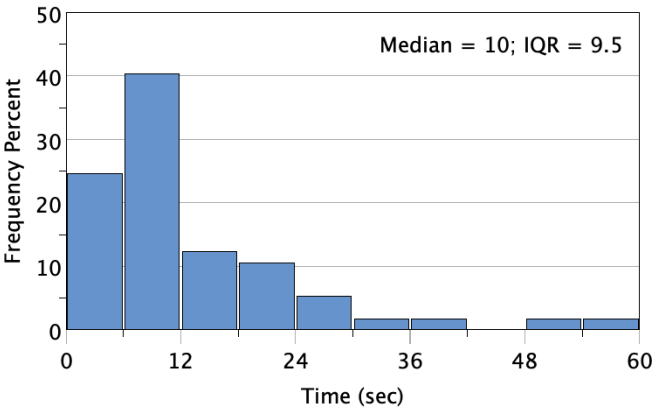
Energetic plausibility of over-water foraging

I developed a model to evaluate the costs and benefits of hover-gleaning decapods by Great-tailed Grackles. Assuming crab sizes similar to those observed in this study (16.9–19.4 mm carapace width) and conservative digestibility estimates for crab tissue and shell (50% and 0%, respectively), the model estimates that an average-sized female grackle would realize a net energy gain of 244–445 J after accounting for the average foraging time per successful capture (Fig. 4). Under this conservative scenario, net energy gains become negative only when crabs are at least 46% smaller (< 9.7 mm carapace width) or when average foraging time per successful capture is more than 126% greater than observed (e.g., > 48.5 s per successful foraging excursion). For comparison, a male grackle averaging 230 g would realize a net energy gain of 115–316 J from consuming an average-sized crab under the same conservative digestive scenario (Fig. 4). Estimated gains were greater under less conservative assumptions about digestibility; for example, a female grackle consuming an 18 mm wide crab would realize an estimated net energy gain of approximately 771 J if 75% of soft tissues and 25% of hard parts were digested.

DISCUSSION

My observations indicate that brown-plumaged (presumed female) Great-tailed Grackles on Isla Cozumel forage decapods from floating sargassum, a newly emergent habitat within their established geographic range. This behavior raises questions about its novelty, constraints, and energetic feasibility.

Fig. 3. Histogram of foraging durations (n = 57).



Novelty of foraging behavior

Many aspects of over-water foraging exhibited by Great-tailed Grackles differ in distinct ways from those previously reported for Great-tailed Grackles and other icterids. Chiefly a ground forager, the Great-tailed Grackle forages in a wide variety of terrestrial habitats, including fields, marshes, beaches, lawns, parking lots, feedlots, agricultural fields, and orchards. Great-tailed Grackles are also known to forage for tadpoles and small fish while walking in shallow water (Miller and Winn 1951, Skutch 1954). Most accounts of grackles foraging for fish over deeper water (e.g., Skutch 1954, Skutch 1958, Johnson and Peer 2022) appear to trace back to a single second-hand report of Great-tailed Grackle seizing minnows from the water surface while flying, and diving to shallow depths "like a tern or kingfisher" (Anthony, as cited in Griscom 1932:400).

There are also several reports of fishing behaviors among other species of grackle. McIlhenny (1937:289) notes that small fish, frogs, and other water creatures from ponds, ditches and marshes are among the favorite foods of the Boat-tailed Grackle (*Quiscalus major*), and that they thrust "their head completely below the surface in order to secure any small water creature" and that females "frequently hover over shallow water, swooping down gull-like... without touching their bodies to the water." Similarly, Sprunt (1958:369) describes the Boat-tailed Grackle as a wader in shallow water that it also "hovers like a petrel." Carib Grackles (*Quiscalus lugubris*) forage for fish with their beaks while perched on mangrove roots (Rodriguez-Ferraro 2016), and there are reports of Common Grackles (*Quiscalus quiscula*) hovering over water to catch small fish (Beeton and Wells 1957, Zottoli 1976). So, although there are several reports of in-water and over-water foraging for fish by some other members of the icterid family, there are no previous reports of foraging for decapods from floating macroalgae. Taken together, these comparisons support the conclusion that hover-gleaning decapods from floating sargassum represents a previously undescribed foraging strategy and habitat use for Great-tailed Grackles within their established range.

Mechanics and constraints of foraging

The structured sequence of behaviors exhibited by the Great-tailed Grackles suggests a consistent foraging strategy. The five different foraging phases occur in consistent sequences, defining four types of foraging events. Successful foraging events (Type 1) include all five phases and can include multiple cycles of searching and hovering phases. Foraging events that do not include gleaning (Type 2) or hovering and gleaning (Type 3) phases suggest that the grackle was unable to glean or find the prey, respectively. Type 4 foraging events include only the outbound and inbound flight phases, without searching, hovering, or gleaning, and their purpose remains unclear. Because Great-tailed Grackles rarely fly over the ocean, except to forage over sargassum or as a shortcut across small bays, Type 5 behaviors might represent a more limited attempt to forage when conditions are unfavorable or when experience is lacking.

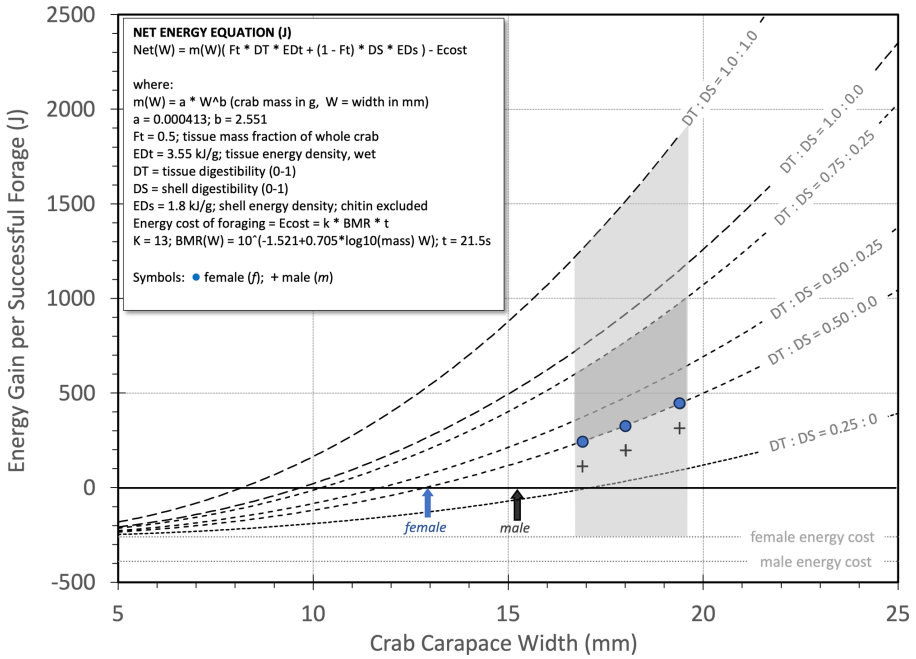
In Cozumel, this hover-gleaning behavior appears to be a sex-specific behavior practiced exclusively by brown-plumaged (presumed female) grackles. Although possibly a misidentification or sampling artifact resulting from the limited scope of this study, other plausible explanations might include morphology and life history. To explain the lower proportion of animal material in male grackle diets, Davis and Arnold (1972) suggested that the greater size and larger tail of the male Great-tailed Grackle may make it less agile and maneuverable. I observed male grackles attempting to steal crabs from returning brown-plumaged grackles on several occasions, suggesting that males consider *Portunus sayi* to be a desirable food source, but I never observed a male grackle engaging in hover-gleaning. It is also conceivable that the greater nutritional demands during breeding season cause female grackles to seek higher protein food sources (Davis and Arnold 1972). Following the formal observation period of this study, I opportunistically observed brown-plumaged grackles foraging over sargassum as early as late March and as late as early September, consistent with both the seasonal abundance of sargassum (March–October) and the breeding cycle (mid-March to mid-July; Johnson and Peer 2022). If a sex-specific behavior, it would appear consistent with McIlhenny's (1937) description of hover-gleaning by female Boat-tailed Grackles.

The novel behavior used by Great-tailed Grackles bears similarities with foraging strategies of some terrestrial passerines and seabirds (e.g., DeGraaf et al. 1985, Remsen and Robinson 1990). In contrast with more typical hover-gleaning behavior, the Great-tailed Grackle extends its toes to the sargassum while gleaning, but the water rarely reaches the tibial feathers. In this sense, the grackle behavior is more akin to a "hover-touch glean." Some seabirds (e.g., storm petrels) that seize prey from the water surface utilize "pattering" (e.g., Kees and Garthe 2004) to achieve weight support, forward locomotion, and stabilization (Xue et al. 2023). In the case of the Great-tailed Grackle, there is no forward motion at the time of prey capture, so contact with the floating algae might provide a small amount of buoyancy or frame of reference while gleaning in the dynamic environment of the air-water interface. Regardless of the aerodynamic mechanism, the repeated sequence of phases that comprise the different types of foraging events suggest that conditions at the air-water interface, in addition to the accessibility of sargassum rafts and prey, strongly constrain success.

Energy considerations

The model results indicate that capture and consumption of sargassum swimming crabs by Great-tailed Grackles could yield positive net energy returns across a range of plausible assumptions and conservative digestive scenarios. This supports

Fig. 4. Plot of net energy gain of successful forages as a function of crab size. Curves show the net energy gains for female grackles over a range of crab sizes and different tissue (Dt) and shell (Ds) digestive scenarios. The lowest curve, modeled after a conservative scenario based on human processing and consumption, illustrates the net energy gain if a grackle digests only 25% of soft parts (12.5% wet mass); the uppermost curve illustrates the limit of net energy gained based on a theoretical scenario in which the grackle completely digests all soft and hard parts. Filled circles show the estimated energy gains for female grackles and crosses indicate those for males. The light gray polygon outlines the energy gains resulting from a range of foraging and digestive; the dark gray shading indicates energy gains resulting from successful forages and conservative scenarios considered likely. Arrows indicate break-even crab sizes for female and male grackles, assuming a digestive scenario of soft to hard parts = 0.50 : 0.0.



the conclusion that over-water hover-gleaning for decapods is energetically feasible for the foraging conditions observed in this study. However, these estimates should be considered preliminary because few data are available for this specific situation, including the energetic cost of grackle flight, energy density of sargassum swimming crabs, and the digestibility of crab tissue and shell by Great-tailed Grackles. As a result, the model relies heavily on proximate examples and should be viewed as a plausibility study rather than a precise estimate of energetic consequences.

The seasonal availability of sargassum suggests that sargassum swimming crabs are unlikely to become a major part of the Great-tailed Grackle diet. However, the crabs expand the resource base available for this opportunistic species. Foraging for crabs requires some travel costs, specialized handling, and risk, yet the crabs are predictably present, relatively abundant in the floating sargassum, and provide substantial energy gains. By comparison, terrestrial insects such as grasshoppers offer higher energy and require less travel, although search and handling costs may be greater. Human refuse (e.g., a tortilla chip) can yield tremendous energy rewards and requires little travel or specialized handling, but is highly unpredictable in time and space. Overall, the model results support the conclusion that when floating sargassum is accessible and crabs are of typical size, hover-gleaning can yield appreciable net energy gains despite the added costs of travel, handling, and environmental risk.

Ecological drivers and geographic scope

This section addresses three questions: why now?, why here? (including prey availability), and where else?, to explain constraints on the feasibility of this novel foraging behavior. Historical net tows (Butler et al. 1983, Schell et al. 2015), satellite images (Wang and Hu 2017, Johns et al. 2020), and stakeholder interviews (Rosellón-Druker et al. 2023) all reveal only small areas of sargassum in the Caribbean Sea prior to 2011. The marine macroalgae habitat, which is increasing globally (Qi et al. 2025), became a dominant feature of the western Caribbean after 2014–2015 and Great-tailed Grackles apparently took advantage of it.

Local environmental factors likely influence where Great-tailed Grackles practice this novel foraging behavior by affecting both the accessibility of floating sargassum (e.g., its persistence in the nearshore zone) and the suitability for foraging (e.g., raft size and continuity, proximity to breaking surf, decomposition following stranding). In western Cozumel, floating sargassum is generally less abundant and frequent than along windward coastlines, but the more sheltered coastline may make sargassum rafts more accessible and over-water foraging more favorable. I infer that the wind and waves at this site, together with the Yucatan Current (Chávez et al. 2003), may influence the daily to seasonal changes in sargassum distribution. Taken together, these observations are consistent with the idea that this behavior emerged where abundant rafts of sargassum were both accessible and suitable for foraging.

The prey ecology of the sargassum habitat likely also constrains foraging behavior. The dominant prey captured by grackles from floating sargassum is the sargassum swimming crab (*Portunus sayi*), which could reflect prey abundance, a dietary preference, or ease of foraging and capture. Only once (23 April 2023) have I observed a grackle returning to shore with prey other than a crab: a Sargassum Frogfish (*Histrio histrio*). In the Caribbean, arthropods (mostly shrimp) comprise about 60% of the individuals in floating sargassum, whereas *Portunus sayi* averages one to four individuals per kg of wet sargassum (van Tussenbroek et al. 2024a, 2024b). Although amphipods, shrimp, and snails are more abundant, their smaller size (< 1 cm) makes them more challenging foraging targets and a likely lower energy gain than *P. sayi*. The larger frogfish would yield a much higher energy gain, but it is less abundant (0.12–0.25 individuals per kg; Corbin et al. 2024). In summary, *Portunus sayi* may not be the most abundant type of prey, but it is among the most energetically profitable prey that can be readily gleaned by grackles.

Preliminary observations at several additional sites suggest patterns of environmental conditions that constrain other locations where over-water foraging behavior might be utilized. In eastern Cozumel, Great-tailed Grackles regularly pick through beached sargassum, but I have never observed over-water foraging along this more exposed coastline, perhaps because floating sargassum rarely persists outside the surf zone before getting beached. In Playa del Carmen, another windward coastline, I have occasionally observed grackles foraging from a long pier along nearshore barriers that trap floating sargassum outside the surf zone (> 100 m from shore). Grackles also use over-water foraging in San Pedro, Belize, where the Mesoamerican Reef protects this windward nearshore environment. During June 2025, I observed several brown-plumaged grackles using the same foraging strategy described from Cozumel to capture *Portunus sayi* from floating sargassum among the many shoreline structures. These site comparisons support the idea that the foraging strategy is most feasible where nearshore sargassum is persistent and readily accessible, enabling repeated short excursions to capture energetically profitable prey.

Implications for adaptability

This study adds to the literature on the many foraging strategies used by Great-tailed Grackles. Whereas most research on grackle flexibility has focused on adaptations associated with range expansion that occurs when grackles encounter new geographic regions, climates, resources, and competitors through dispersal at the edge of their range, this example from Cozumel is more consistent with an opportunistic response to rapid ecological changes that emerged within an established geographic range.

A key unresolved issue is whether this regionally distributed foraging behavior originated by separate innovations (e.g., Ducatez et al. 2013), or whether it originated at a single site and spread through transmission (e.g., Lefebvre 1995, Aplin et al. 2015). I am not aware of evidence for frequent movement of grackles across the ~18 km Cozumel Channel, and the distance from the northern Yucatan Peninsula to Ambergris Caye is considerable (~300 km). The relative isolation of the western Caribbean sites where grackles use over-water foraging would seem to imply repeated innovations, but distinguishing from among the alternative explanations will require data on movement, relatedness, and the spatiotemporal pattern of occurrence. Knowledge and skills developed from foraging among beached sargassum might also transfer into an over-water skill, and once learned the behavior could diffuse locally through social learning and repeated practice. Regardless of origin, the observations presented here demonstrate that when floating sargassum is accessible, Great-tailed Grackles can incorporate this pelagic resource into their foraging repertoire.

Limitations and future directions

The opportunistic observations described here were made by a single observer at a single site and therefore provide a foundational survey rather than a comprehensive investigation. The primary contribution is to document a novel foraging behavior and motivate future study of its geographic extent and ecological constraints. Individual birds were unmarked and unidentified, so the local prevalence of the behavior (i.e., proportion of individuals at the site) needs further study. The limited duration of the study also precludes conclusions about the relationship of this behavior to the breeding cycle. Although informal observations confirm that Great-tailed Grackles also forage for decapods elsewhere in the western Caribbean, systematic surveys are needed to evaluate where this behavior occurs, and under what conditions. Observations of juvenile behavior, mother-offspring interactions, and geographic distribution may help illuminate the roles of behavioral flexibility, innovation, and social transmission in within-range adaptations.

CONCLUSION

This study provides a first description of Great-tailed Grackle foraging for decapods over floating sargassum, an atypical behavior for terrestrial icterids. Along the western shoreline of Cozumel, brown-plumaged grackles use a consistent sequence of flight modalities to capture sargassum swimming crabs while hovering over sargassum rafts. Together, the observed capture success, short excursion durations, and energetic model indicate that this foraging strategy is a plausible and potentially profitable use of floating sargassum as a foraging habitat.

Recurring sargassum inundations beginning in 2014 to 2015 likely enabled this behavior by making a pelagic resource seasonally accessible in the nearshore zone. Although this study focused on Cozumel Island, additional observations suggest this behavior occurs at several other western Caribbean sites. In contrast with studies linking grackle flexibility to range expansion, this study illustrates how flexibility may also support within-range responses to rapid ecological change. Future research should examine environmental and social drivers of participation and learning pathways.

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Data Availability:

The final data (.csv), energetics model (.xlsx), and additional media that support this study are openly available from Wirth (2026) at the Open Science Framework: https://doi.org/10.17605/OSF.IO/W6E8Y.

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APPENDIX

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Additional Details of Energy Calculations

Crab Carapace Width - To estimate the energy content of sargassum swimming crabs captured by grackles in this study, I first had to estimate the sizes of the crabs. This was accomplished by comparing the width of the crab carapace (CWp) with the length of the grackle beak (GBp) in photographs where both crab carapace and beak were sub-parallel to the camera sensor. The width of the crab carapace (W) was then determined by multiplying the carapace width in the photo (CWp) / beak length in the photo (GBp) times the average beak length of female Great-tailed Grackles (GBavg = 22 mm; Johnson and Peer, 2022).

Crab Wet Mass - Next, I had to estimate the mass of the observed sargassum swimming crabs. Only limited paired data are available for the size and mass of sargassum swimming crabs (West and Brooks, 2018), so I supplemented the published data with unpublished measurements from a nearby study (V. Monroy Velazquez, pers. commun.). I then determined the width-mass constant (a) and exponent (b) of the power-law relationship by regression. Finally, I estimated the wet masses (m[W]) of the observed crabs using the estimated carapace width (W) and the power law relationship (m[W] = a * W^b).

Energy Content of Sargassum Swimming Crabs – The effective digestible energy of sargassum swimming crabs is unknown but can be estimated using data for a blue crab proximate. The fraction of blue crab that is tissue (Ft) depends in part on growth stage and is estimated to range from 0.15-0.5 (Fuso et al., 2025). Based on studies of passerine, poultry, and seabirds, I estimated the digestibility of tissue (DT) to range from 0.5-1.0 (Potter et al., 1962; Twedt, 1985). Analyses of the energy density of tissue (EDt) of blue crab indicate a range from 3.5-4.2 $kJ \cdot g^{-1}$ wet (USDA 2026 nutrient data, NDB 100330). The digestibility of shell (DS) is estimated to range from 0-0.5 based studies of seabirds (Jackson et al., 1992; Barrett et al., 2007). Although it is unknown whether Great-tailed Grackle can extract the energy content of the crab hard parts, I nonetheless estimated the energy content of the shell to assess its potential impact on the energy calculations. Using protein (Ps), lipid (Lw), and chitin (Cw) fractions of a blue crab proximate (Fuso et el., 2025), and Atwater factors (Afp, Afl, Afch, respectively) for each of these components (FAO Food and Nutrition Paper 77 (2003), I calculated the energy density of shell (EDs = Afp * Pw + Afl * Lw + Afch * Cw * DFch). The digestibility of chitin is adjustable in the model (DFch) but assumed to be near zero for icterids. Finally, I estimated the effective digestible energy (K) using the following: K = Ft * DT * EDt + (1-Ft) * DS * Eds.

Energy Cost per Successful Forage – The average female Great-tailed Grackles has a mass (m) ~130 g (Johnson and Peer 2022), with an estimated basal metabolic rate (BMR = 10^(-1.521 + 0.705 * LOG10(m))) of ~0.93 W (Lasiewski and Dawson 1967, McKechnie and Wolf 2004). Using data from passerine scaling studies (Bishop 1999, Ward et al. 2001), I assume an average flight multiplier (k = 13) to estimate the energetic costs of forward flight and hovering (k x BMR). Based on an average mass of 203 g (Johnson and Peer, 2022), male grackles are estimated to have a BMR of 1.39 W. I then used the observed average foraging time per success (t - 21.5 s) to estimate the energetic cost of foraging flight (Ecost = k * BMR * t).

Net Energy Cost per Successful Forage – Finally, the net energy gain of a successful forage (Net(W)) can be estimated from the mass of the sargassum swimming crab prey, the effective digestible energy density of the crab, and the energy cost of foraging flight (Net(W) = m(W) * K - Ecost). The model permits adjustment of many of parameters (e.g., crab size, tissue weight fraction, fraction of digestible tissue, fraction of digestible shell, average foraging time, flight multiplier, etc.) to evaluate their sensitivity of the model to each.

Table A.1. List of dates, start times, durations of observation sessions, and ID numbers of eBird checklists from each session. Photographs from observation sessions can be accessed from the Macaulay Library using the checklist IDs (e.g., *https://ebird.org/checklist/S115695958*).

Date	Start Time (EST)	Duration	eBird Checklist IDs
24-Jul-22	07:45	109	S115695958
30-Jul-22	12:18	47	S116029317
30-Jul-22	14:00	59	S116036332
31-Jul-22	08:43	17	S116080044
31-Jul-22	11:02	61	S116101765
31-Jul-22	12:48	30	S116101759
01-Aug-22	09:57	30	S116155204
01-Aug-22	19:04	27	S116216594
02-Aug-22	11:44	34	S116241287
02-Aug-22	19:10	13	S116242713
04-Aug-22	06:20	50	S116346192
05-Aug-22	07:40	51	S116378528
05-Aug-22	11:09	10	S116377158
05-Aug-22	18:40	40	S116399909
06-Aug-22	08:26	40	S116428155
06-Aug-22	18:33	38	S116460502
08-Aug-22	19:04	30	S116638895
10-Aug-22	08:28	60	S116669909
11-Aug-22	08:01	30	S116719661
11-Aug-22	09:28	33	S116719654
14-Aug-22	07:52	40	S116903882
14-Aug-22	10:45	46	S117036899
15-Aug-22	18:39	15	S117036909
17-Aug-22	15:04	65	S117113846
19-Aug-22	18:55	17	S117236168
21-Aug-22	08:57	74	S117332724
21-Aug-22	19:10	10	S117410208
22-Aug-22	18:48	37	S117415507

Table A.2. Parameters and equations used for energy calculations.

Symbol	Parameter	Value / Range	Units	Source
E1. Width of Crabs from Photos; this study				
W = CWp / GBp x GBavg				
CWp	Carapace width in photo	*measured*	*mm*	Measured from photographs; this study
GBp	Grackle Beak Length in photo	*measured*	*mm*	Measured from photographs; this study
GBavg	Beak Length of Female Grackle	22	mm	Johnson and Peer (2022)
W	Crab carapace width	-	mm	derived, this study
E2. Crab Mass from Width & Regression Parameters				
m(W) = a * W^b *(used first with paired P. sayi length & weight data to determine a & b; then used to solve for wet mass of P. sayi this study)*				
W	Carapace width	6-39	mm	West & Brooks (2018); V. Monroy Velazquez, pers. communication
a	Width-mass constant	0.00059	-	regression, this study
b	Width-mass exponent	2.428	-	regression, this study
m(W)	Crab wet mass	0.05-4.3	g	calculated from width estimates from photographs using regression values derived from publ. width and mass pairs
E3. Energy Density of Crab Shell				
EDs = 17 * Pw + 37 * Lw + 17 * Cw * DFch				
Pw	Protein fraction (wet)	0.0733	$g \cdot g^{-1}$	Blue crab proximate composition; Fuso et al. (2025)
Lw	Lipid fraction (wet)	0.015	$g \cdot g^{-1}$	Blue crab proximate composition; Fuso et al. (2025)
Cw	Chitin fraction (wet)	0.1075	$g \cdot g^{-1}$	Blue crab proximate composition; Fuso et al. (2025)
DFch	Digestibility of chitin	0-1	–	Adjustable; assumed near zero for icterids
Afp	Atwater factor for protein (kJg)	17	-	FAO Food & Nutrition Paper 77 (2003)
Afl	Atwater factor for lipids (kJg)	37	-	FAO Food & Nutrition Paper 77 (2003)
Afch	Atwater factor for chitin (kJg)	17	-	FAO Food & Nutrition Paper 77 (2003)
EDs	Energy Density of crab shell	-	$kJ \cdot g^{-1}$ wet	Derived from proximate analyses

E4. Energy Density of Whole Crab				
K = Ft * DT * EDt + (1-Ft) * DS * EDs				
Ft	Tissue fraction of whole crab	0.15–0.50	–	Anatomy estimates & from Blue Crab proximate; Fuso et al. (2025)
DT	Digestibility of Tissue	0.5–1.0	–	Passerine/poultry/seabird studies; Potter et al. (1962; Twedt (1985)
EDt	Energy Density of tissue	3.5-4.2	kJ·g⁻¹ wet	USDA 2026 nutrient data, NDB 100330
DS	Digestibility of Shell	0–0.5	–	Seabird studies; Jackson et al. (1992); Barrett et al. (2007)
EDs	Energy Density of shell	~0.6–1.8	kJ·g⁻¹ wet	As above; protein and lipid only (excl. chitin)
K	Effective digestible energy	*derived*	J·g⁻¹	From E4
E5. Energy Cost per Successful Forage				
BMR = 10^(-1.521 + 0.705 * LOG10(m))				Lasiewski & Dawson (1967); Bennet and Harvey (1987); McKechnie & Wolf (2004)
Ecost = k * BMR * t				
m	Body mass	130-230	g	Johnson & Peer 2022; Female avg = 130 g, Male avg = 230 g
BMR	Basal metabolic rate	*derived*	W	From E5; Female = 0.93, Male = 1.39
k	Flight multiplier	~13	–	11-16x from Ward et al. (2001) and Bishop (1999)
t	Foraging time per success	21.5	s	This study; total foraging time / no. successful forages
Ecost	Flight energy cost	*derived*	J	this study; Female = 260, Male = 389
E6. Net Energy per Successful Forage				
Net(W) = m(W) * K - Ecost				
m(W)	Crab wet mass	From E2	g	From E2
K	Effective digestible energy density	From E4	J·g⁻¹	From E4
Ecost	Flight cost per capture	From E5	J	From E5; Female = 251, Male = 368
Net(W)	Net energy gain	*derived*	J	From E6

Figure A.1. Plot of number of Great-tailed Grackle foraging events (per hour) over floating sargassum during the period of observation (07 July – 21 August). Days without any recorded foraging events indicate a lack of sargassum because grackles generally forage whenever sargassum is present and suitable for foraging.

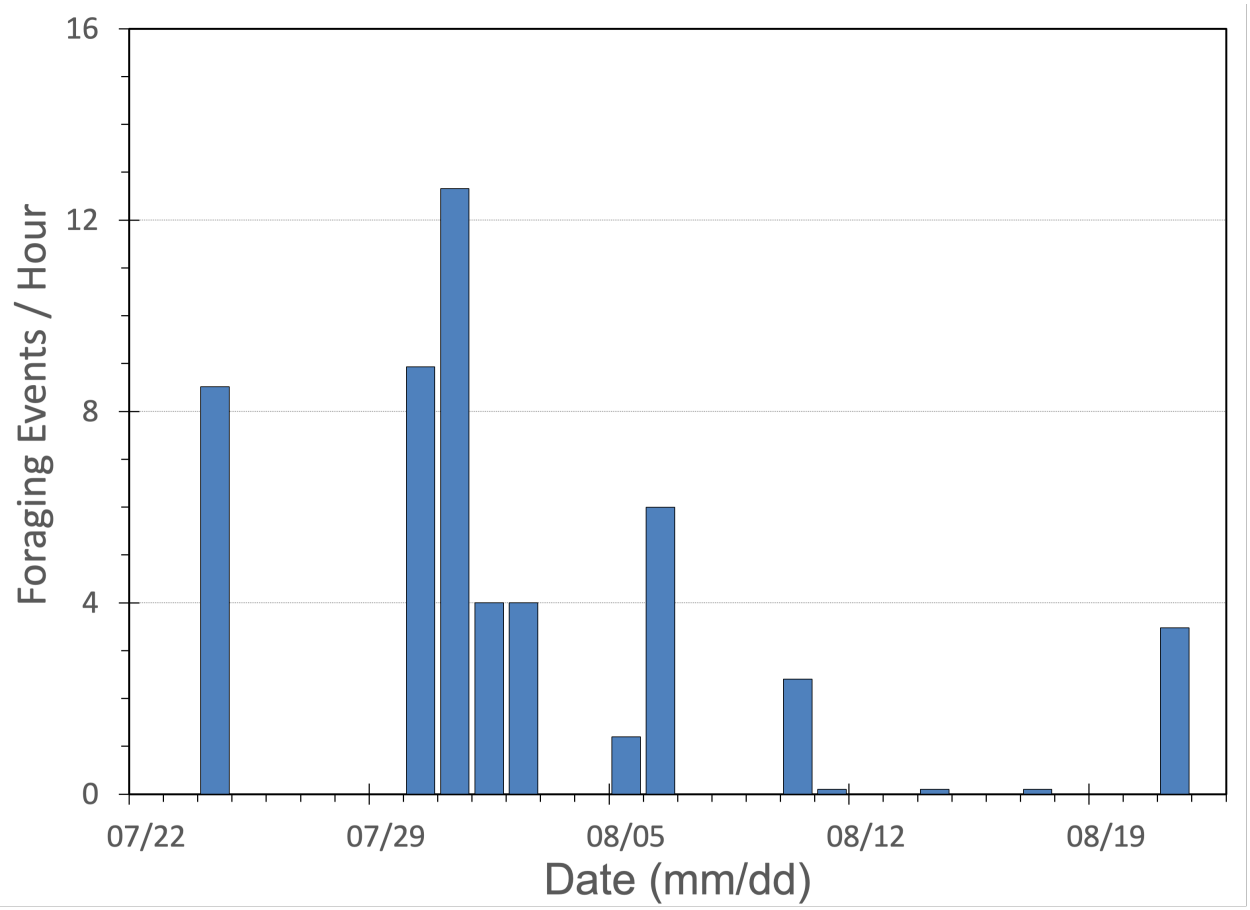
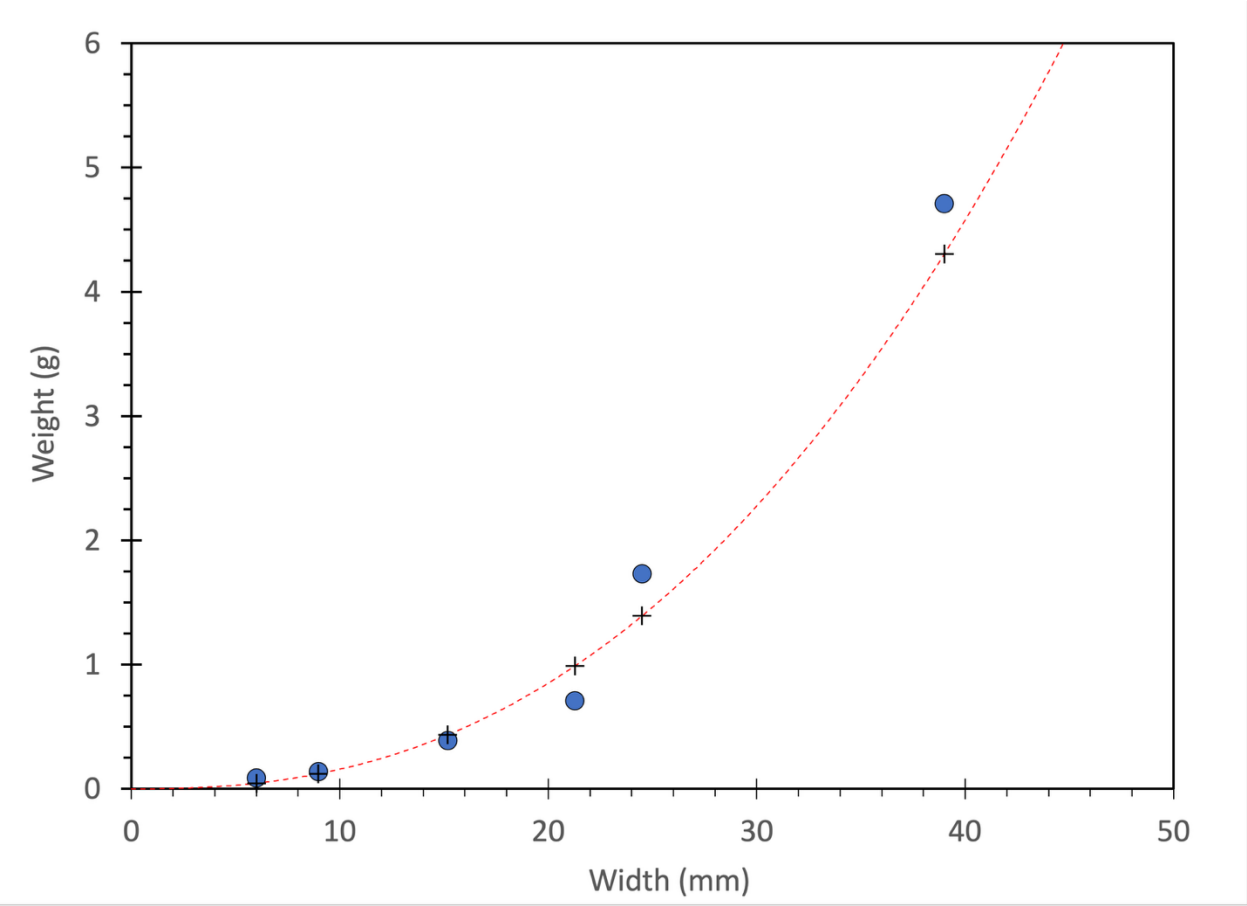


Figure A.2. Crab Width and weight data (filled blue circles) for sargassum swimming crabs from the literature (West and Brooks, 2018) and from V. Monroy Velazquez (unpublished data, 2025). The relationship between crab weight and carapace width is modeled as a power law function (red dashed line). Modeled weights of measured crabs are indicated with plus ('+') symbols.



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