

Research



Cite this article: Perevolotsky T, Martin CH, Rivlin A, Holzman R. 2020 Work that body: fin and body movements determine herbivore feeding performance within the natural reef environment. *Proc. R. Soc. B* **287**: 20201903. <http://dx.doi.org/10.1098/rspb.2020.1903>

Received: 6 August 2020

Accepted: 19 October 2020

Subject Category:

Morphology and biomechanics

Subject Areas:

biomechanics, ecology

Keywords:

herbivorous fish, fish feeding, body kinematics, biting

Author for correspondence:

Roi Holzman

e-mail: holzman@tauex.tau.ac.il

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5189532>.

Work that body: fin and body movements determine herbivore feeding performance within the natural reef environment

Tal Perevolotsky^{1,2}, Christopher H. Martin^{3,4}, Asaph Rivlin² and Roi Holzman^{1,2}

¹School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel

²The Inter-University Institute for Marine Sciences, POB 469, Eilat 88103, Israel

³Department of Integrative Biology, and ⁴Museum of Vertebrate Zoology, University of California, Berkeley, CA, USA

TP, 0000-0002-9630-3027; CHM, 0000-0001-7989-9124; RH, 0000-0002-2334-2551

Herbivorous fishes form a keystone component of reef ecosystems, yet the functional mechanisms underlying their feeding performance are poorly understood. In water, gravity is counter-balanced by buoyancy, hence fish are recoiled backwards after every bite they take from the substrate. To overcome this recoil and maintain contact with the algae covered substrate, fish need to generate thrust while feeding. However, the locomotory performance of reef herbivores in the context of feeding has hitherto been ignored. We used a three-dimensional high-speed video system to track mouth and body kinematics during *in situ* feeding strikes of fishes in the genus *Zebra-soma*, while synchronously recording the forces exerted on the substrate. These herbivores committed stereotypic and coordinated body and fin movements when feeding off the substrate and these movements determined algal biomass removed. Specifically, the speed of rapidly backing away from the substrate was associated with the magnitude of the pull force and the biomass of algae removed from the substrate per feeding bout. Our new framework for measuring biting performance *in situ* demonstrates that coordinated movements of the body and fins play a crucial role in herbivore foraging performance and may explain major axes of body and fin shape diversification across reef herbivore guilds.

1. Introduction

Feeding is a complex task, requiring the coordinated operation of multiple functional systems, working in concert to locate, pursue, capture, process, digest and assimilate resources [1–3]. Successful feeding requires the integration and control of the locomotory, sensory and prey capture systems. Because feeding success is tightly linked to the individual's fitness, the functional tasks that affect it are expected to be under strong selective pressures. Indeed, morphologies that enhance locomotory performance on the one hand, and prey capture and processing on the other hand, are often considered major axes of vertebrate diversification [2,4–8], and are expected to co-evolve in response to the functional demands of feeding and locomotion. In birds, both the aspect ratio of the wings and beak morphology are strong predictors of the bird's trophic niche [7,9–11]. For example, nectar-feeding birds are characterized by a thin long beak and high-aspect ratio wings, whereas raptors are characterized by wings with intermediate aspect ratio, and short, sturdy, curved beaks [12,13]. The functional coupling of locomotory apparatus (e.g. wings, legs or fins) and prey capture apparatus (e.g. teeth, beaks, talons or claws) is most evident in predators of mobile, evasive prey [5–7]. By contrast, this functional coupling might be less evident in animals that feed on non-motile prey. In herbivores, functional diversification is mostly explained based on the adaptation of their feeding apparatus (e.g. teeth and jaws) to shear, tear, cut and grind plant material [14–17], and adaptations of the digestive system to process and



Figure 1. Documenting *in situ* feeding kinematics of herbivorous reef fishes feeding in the Red Sea. (a) An aerial view of the fringing reef and algal turfs at the study site, the Interuniversity Institute for Marine Sciences (IUI) in Eilat, Israel. (b) The underwater video system, positioned on the algal turf, was comprised of two high speed cameras and a synchronized force transducer. The system allowed the three-dimensional tracking of the movements of the fish's body, fins and mouth during feeding, while simultaneously measuring the forces they exerted on a feeding plate naturally colonized by turf algae. (c) We focused on two species of Acanthuridae, *Zebrasoma xanthurum* (left) and *Zebrasoma desjardini* (right), both characterized by a deep body shape, elongated dorsal and anal fins, protruding snout and a small mouth, as well as serrated teeth that allow them to tear algae. Photos by (a) Yoav Lindman and (c) François Libert. (Online version in colour.)

digest it [18–21]. Herbivore locomotory capabilities are traditionally viewed only in the context of spatial movement between food patches and predator avoidance [8,22–25].

Fishes are an excellent model system to study the relationships between form and function, yielding many insights regarding the functional morphology of the feeding and locomotory systems [26–29]. For example, fused teeth and short lower jaws have repeatedly evolved in fishes that crush armoured prey or excavate hard surfaces to access boring organisms [30,31] whereas comb-like teeth enable raking organic material trapped in dense algal mats [14,32]. The locomotory behaviours of ambush predators during feeding strikes are well characterized and rely on explosive, short-ranged movements to capture prey from close distance; including extended jaw protrusion, large gape and strong pectoral fins that are used to accelerate the body forwards [33,34]. The shape of the pectoral fins, namely their aspect ratio, determines the speed of labriform swimmers and has been tightly linked to their habitat use and their location in the water column, but has yet to be linked to their feeding kinematics [35–37]. In herbivores, body shape and fin aspect ratio distinguish between species that feed on large macroalgae and those that scrape encrusting algae from hard substrates [38]. Furthermore, a fusiform body shape and high aspect ratio fins are associated with species that forage in sites exposed to strong currents [38–40]. However, it is still unclear what role the body and fins play in the feeding process of herbivores or other fish that feed from the substrate.

From a mechanical standpoint, the body of an aquatic herbivorous fish should be expected to play an important role in facilitating feeding. When a tearing or shearing force is applied to an alga or a macrophyte, an equal and opposite reaction is applied on the animal. If the body is not anchored to the ground, the ensuing recoil could hinder the fish's ability to cut or dislodge the plant material from the substrate. In the terrestrial realm, these recoil forces are countered by anchoring the body to the ground, and the animal's weight

and muscles are used to produce static forces rather than to generate fast, broad movements. In water, neutrally buoyant fish need to use dynamic forces, rather than static ones, to produce thrust that will counteract feeding recoils and enable successful feeding. In most fishes, this thrust is generated primarily using the pectoral and caudal fins, as well as the body surface itself [41]. Therefore, for fishes that bite from hard substrates, we predict that feeding bouts will be characterized by coordinated movements of the mouth, body and fins. These movements are expected to generate thrust, which affects the force exerted on the substrate and ultimately determines the fish's ability to successfully remove the prey. Indeed, Rice *et al.* [42,43] have noted that such coordination exists in parrotfishes and wrasses. However, it is still unclear as to whether and how these movements generate thrust and facilitate feeding.

In the present study, we describe the body and fin movements of herbivorous fishes while feeding from the substrate *in situ* on an exposed patch of fore reef on the Red Sea. We then quantified how these movements affect feeding performance in the relevant field context. Specifically, we sought to: (i) characterize the kinematics of the body, fins and mouth of herbivorous fishes feeding in the wild; (ii) examine how feeding kinematics influences the forces exerted by fishes on the substrate during feeding; and (iii) examine the relationship between the forces exerted and the amount of algae removed from the substrate. To achieve these goals, we developed a new *in situ* underwater system comprising two high-speed video cameras and a force transducer. The system provides detailed high-speed three-dimensional kinematics, accompanied by synchronized high-resolution measurements of the push and pull forces exerted by the fish on a feeding plate naturally colonized by algae. We focused on two species of roving reef herbivorous fishes, *Zebrasoma xanthurum* (Acanthuridae; Blyth, 1852) and *Zebrasoma desjardini* (Acanthuridae; Bennett, 1836; figure 1). Both species are common in coral reefs across the Indo-Pacific

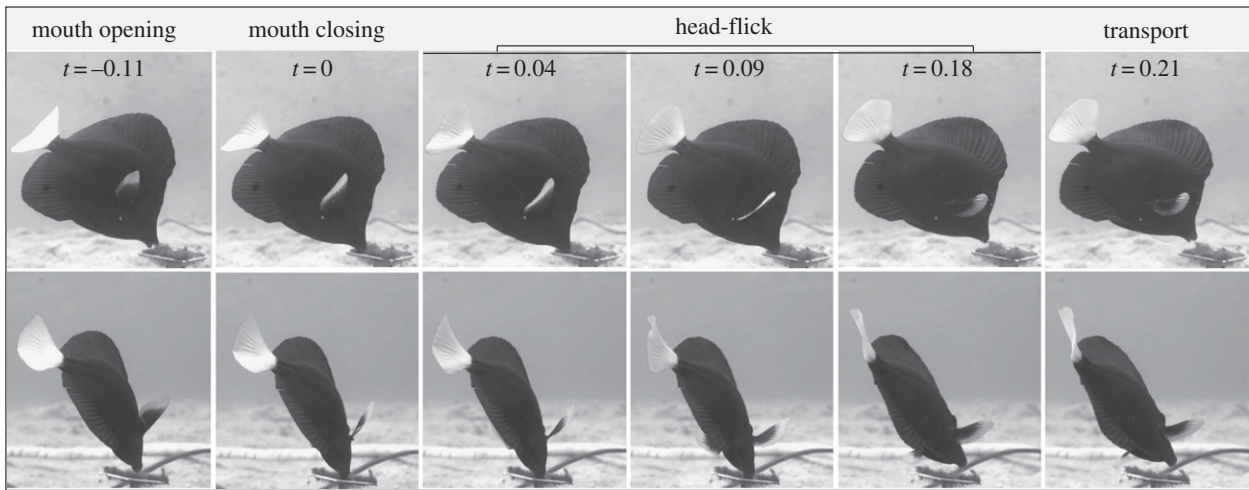


Figure 2. *Zebrasoma xanthurum*, a browsing herbivorous fish, feeding from the substrate. Biting the substrate constitutes a mouth ‘opening phase’ that spans from the initiation of mouth opening until peak gape; a mouth ‘closing phase’ that spans from peak gape until the mouth is closed, and a ‘post mouth closer’ phase in which a rapid ‘head-flick’ is performed upon breaking contact with the substrate. Biting from the substrate is followed by transporting the detached algae into the mouth using rapid mouth opening to generate suction flows. See ‘video analysis’ subsection in the electronic supplementary material for complete description of the phases within a feeding event.

region and are among the most abundant herbivorous fishes at our study site [44]. In the Red Sea, these fish mainly feed from the shallow beach-rock, where turf algae dominates the algal cover [45] (figure 1).

2. Results

(a) Characterization of coordinated locomotory and feeding kinematics during herbivorous biting

We recorded the three-dimensional movements of the body, fins and mouth of the dominant reef herbivores *Z. xanthurum* and *Z. desjardini* freely feeding on turf algae under natural turbulent conditions in the intertidal zone of the Red Sea. We analysed 40 feeding events (18 feeding events performed by seven *Z. xanthurum* individuals and 22 feeding events by nine *Z. desjardini* individuals), in which the fish fed from a plate connected to a force transducer. A feeding event was defined as a single bite from the feeding plate, followed by a transport event, i.e. the movement of detached algae from outside the mouth further into the buccal cavity [46] (electronic supplementary material, movies S1 and S2). The three-dimensional movements of the body, fins and mouth were reconstructed by tracking a set of 13 landmarks (electronic supplementary material, figure S2). Ten of the landmarks were located on the ‘outer contour’ of the fish and were therefore trackable regardless of the fish’s orientation with respect to the cameras. Three landmarks (base and tip of the pectoral fin and the base of the caudal fin) were only visible from either the left or right side of the fish, depending on the fish’s orientation with respect to the cameras. Thus, pectoral fin kinematics were based on only one fin per feeding event (27 right and 13 left). We only analysed feeding events in which all relevant landmarks were visible from both cameras throughout the feeding event.

Our high-speed videos revealed that both *Z. xanthurum* and *Z. desjardini* did not scrape the substrate with their teeth. Rather, these fish closed their mouth on the protruding algal filaments and then, using a sharp sideways movement of the

head (hereafter ‘head-flick’; figures 2 and 3), yanked and tore the filaments from the substrate. Consequently, we categorize this behaviour as browsing, i.e. herbivory that does not involve the mouth contacting the substrate.

Feeding events were defined as a sequence that included the biting of the algae, a ‘head-flick’ and a transport event (figures 2 and 3). Typically, fish approached the plate and oriented themselves head-down, with the dominant axis of movement roughly perpendicular to the plate. Fish opened their mouth well before contact with the plate, with peak gape occurring at 0.067 ± 0.04 s prior to contact (figure 3*a,b*). Gape closing was roughly synchronized with contact (occurring at 0.022 ± 0.035 s) and with the maximum push force applied on the feeding plate (0.033 ± 0.052 s). Closing of the mouth was followed by a head-flick which occurred 0.082 ± 0.034 s after contact and was roughly synchronized with the maximum pulling force applied on the plate (0.088 ± 0.040 s). The head-flick was accompanied by a forward motion of either both pectoral fins (29 of the 40 events) or the fin on the body side of the movement (i.e. the right pectoral fin when flicking the head to the right; 10 of 40 events). Additionally, the head-flick was accompanied by the movement of the caudal fin towards the same direction as the head in 31 of the 40 events, while in nine other events the tail-body angle did not change during the head-flick.

Following retraction from the plate, fish rapidly opened their mouth, generating suction flows that transported the detached algae into the mouth. At least one such transport event was evident in all 40 digitized feeding events, as well as in more than 100 events that could not be digitized. We used the coupling of biting and transport to compare the kinematics of biting from the substrate to that of suction-feeding within the same individual and during the same feeding event. We hypothesized that fish will display characteristic body kinematics only during the bite. Indeed, a discriminant function analysis revealed that the mouth and body kinematics clearly distinguished between feeding from the substrate and transport events (error rate = 3.9%; 73 of 76 events correctly assigned; figure 4; electronic supplementary material, tables S1 and S2). Transport events were

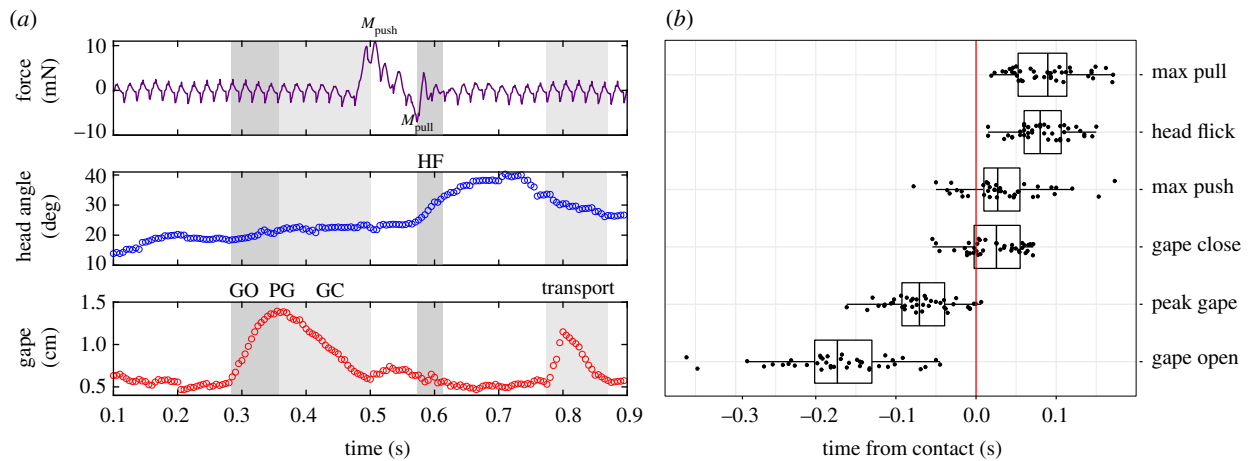


Figure 3. Stereotypic mouth and body kinematics are reflected in the force exerted on the substrate. (a) An example from a single feeding event, depicting gape size, head angle with respect to the body, and the force exerted on the substrate throughout the event. A compression (push) force is assigned positive values and tension (pull) assigned negative ones. Grey shading represents the different phases of the feeding event (figure 2; see the electronic supplementary material, ‘video analysis’). GO, gape opening; PG, peak gape; GC, gape closing; HF, head-flick. The mouth is opened twice during the feeding event, once before biting the algae and once for prey transport. (b) The distribution of the timing of events during 40 bites, standardized to the time of contact with the feeding plate (i.e. contact defined as $t = 0$). Mouth opening occurs well before contact with the substrate, which coincides with mouth closing and peak push force. Peak pulling force is associated with the lateral movement of the head during ‘head flick’. Data is for 40 bites from 16 fishes. Boxes encompass first to third quartiles, horizontal line is the median, whiskers are 1.5 times the inter-quartile range. (Online version in colour.)

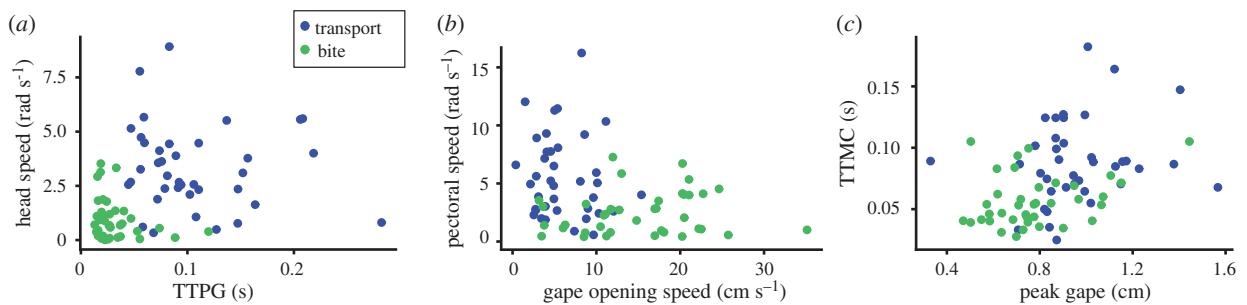


Figure 4. Bites are characterized by fast body kinematics whereas transport events are characterized by fast mouth kinematics. A discriminant function analysis (error rate = 0.039; 73 of 76 events correctly assigned) revealed that bite and transport kinematics are significantly discriminated based on four mouth-related and two body-related variables: (a) time to peak gape was faster during transport while the post mouth-closure (PMC) angular speed of the head was faster following bites, (b) gape opening speed was faster during transports and the PMC angular speed of the pectoral fin was faster following bites, and (c) time to mouth closing (TTMC) was faster during transport, whereas peak gape was larger during bites. PMC head and pectoral fin angular speeds were measured starting when the fish broke contact with the feeding plate (for biting; also termed ‘flick phase’), or once the mouth was completely closed (for transport). The duration of the measurement was 0.04 s in both cases. (Online version in colour.)

distinguished by faster gape opening speed, smaller peak gape, and shorter times to peak gape and mouth closure. Substrate-feeding was distinguished by fast movements of the body and fins including rapid head-flick and forward movement of the pectorals, both occurring well after mouth closing (hereafter post mouth closure head and fin angular speeds; figure 4). Taken together, these findings show that grazing turf algae from the substrate is defined by the coordinated movement of the entire body including the mouth, tail, pectoral fins and head. Furthermore, we show that stereotyped body locomotory events associated with substrate feeding extend beyond only the gape cycle, which usually brackets a predatory strike in studies of fish feeding.

(b) Effect of feeding kinematics on force and removal of algal biomass

We predicted that kinematics of the fins and body will influence the forces exerted by fishes on the substrate during feeding, and that these forces will eventually determine the

amount of algae removed from the substrate. Indeed, a mixed-effect generalized linear model indicated that the swimming speed away from the plate was positively and significantly ($p = 0.003$) correlated to maximal pull force (figure 5a; whole model likelihood ratio test $p = 0.047$; marginal and conditional $R^2 = 0.16$ and 0.71, respectively). All other kinematic variables included in the model (e.g. standard length or species, gape diameter, pectoral fin speed; see the electronic supplementary material, ANOVA tables S3 and S4) did not significantly affect pull force. In turn, the pull force was positively and significantly ($p = 0.033$) correlated with the weight of algae removed from the plate during each feeding bout (figure 5b; linear regression on log-transformed-force and weight; empirical $p = 0.015$ estimated by permutation, adjusted $R^2 = 0.16$; each bout consisted of multiple bites). Taken together, these results (figures 4 and 5) show that body movements, rather than mouth kinematics, are the dominant factor in herbivorous browsing from the substrate, determining the pulling force exerted on the algae and, in turn, the amount of algae removed from the substrate.

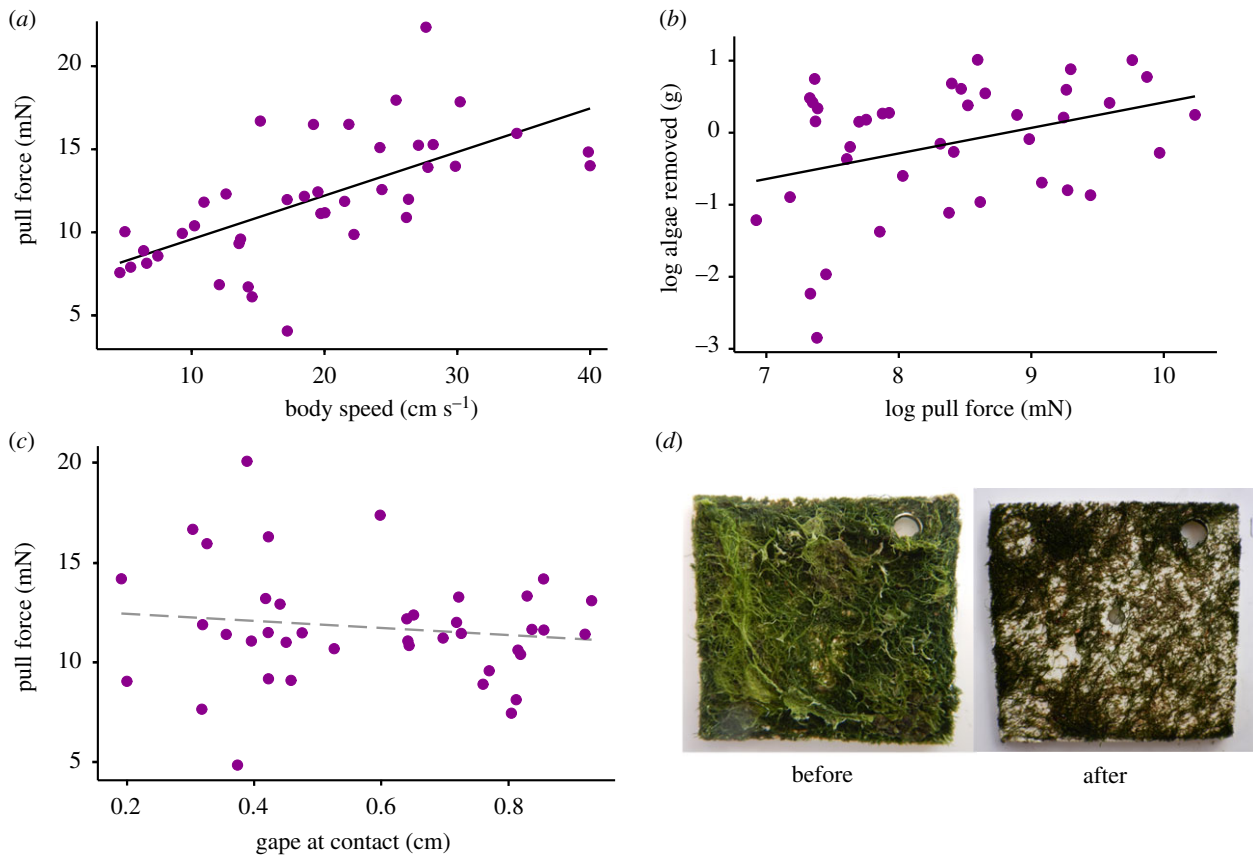


Figure 5. Body speed determines the pull force exerted on the substrate, and that force determines feeding success. (a) Fish body speed post mouth-closure was significantly correlated ($p < 0.004$) with the pulling force exerted on the substrate (linear mixed effect model, $p < 0.05$, marginal $R^2 = 0.17$). Depicted are the partial effects from the mixed-effect model. (b) The log of the total pulling force exerted on the plate was significantly correlated with the log of the total weight of algae removed during a feeding bout (permutation based linear model, $p < 0.015$, $R^2 = 0.16$). (c) The size of fish gape during contact with the algae did not have a significant effect on the pulling force exerted on the substrate. (d) A feeding plate, covered by natural algae, before and after a feeding bout. (Online version in colour.)

3. Discussion

Herbivory plays a pivotal ecological role on coral reefs, maintaining and protecting adult corals from overgrowth by algae while also facilitating coral recruitment by clearing reef substrate [47,48]. Overfishing of herbivorous coral reef fishes results in rapid reef deterioration which can eventually lead to a phase shift, in which the community becomes algal dominated instead of coral dominated [49–51]. Despite the ecological importance, the mechanisms that underlie successful feeding in herbivores are poorly understood. Here we demonstrate that coordinated body and mouth kinematics are a fundamental component of algae-browsing performance in coral reef fishes. We developed an integrated three-dimensional high-speed camera and force system for capturing *in situ* measurements of biting kinematics and performance within the natural reef environment. This system will be broadly applicable for measuring organismal performance in the relevant, but so far highly inaccessible, natural field context in which these performance tasks take place. It is essential to measure how organisms perform these vital tasks in the context of their natural environment to understand the complexity of these behaviours and their relevance to evolutionary fitness [52]. Using this framework, we show that feeding from the substrate is characterized by stereotypic body, head and fin movements (figures 2 and 3); that these movements determine the force exerted on the substrate (figure 5a); and the amount of algae removed from the substrate (figure 5b). Altogether, we

show that body kinematics is the dominant factor that determines feeding performance in browsing herbivores in their natural coral reef environment. Our results contrast expectations arising from studies of suction feeding fishes, where gape kinematics are considered dominant [53,54], and suggests that body morphology and kinematics are an overlooked axis of feeding performance in other fishes that bite the substrate.

Suction feeding is the dominant feeding mode in fishes, in which aquatic predators rapidly reduce the distance between the prey and the mouth while expanding the buccal cavity, protruding the jaws, and generating a flow of water that carries the prey into the mouth [55,56]. Feeding success in suction feeding fishes thus depends on the integration of three hydrodynamic forces: the escape force of the prey, the forward thrust of the predator, and the force exerted by the suction flows [57–60]. By contrast, our results indicate that feeding success in herbivorous browsers depends on the integration of the backward thrust generated by the pectoral fins and the sideways force generated by the head flick, both producing a pulling force that overcomes the tensile strength of the algae, tearing or detaching it from the substrate (figure 5). Subsequently, suction flows are generated to transport the detached algae from the mouth into the buccal cavity. Therefore, the ability of substrate-feeding herbivorous fishes to generate thrust and fast bodily movements after the mouth is closed is a key component in determining their feeding success, rather than the traditional gape opening and closing cycles emphasized in previous studies of fish feeding

kinematics [61]. In fact, it could be that the role of fins and body movements when feeding on suspended prey is also underappreciated, and their functional significance should be re-examined.

Furthermore, we suggest that the traditional categorization of reef herbivores into browsers and grazers needs revision. Reef herbivores are classified as either grazers, which feed on epilithic algal turfs and early successional macroalgae, or as browsers that feed on large protruding macroalgae, select individual algal components and remove only algae and associated epiphytic material with no interaction with the substrate during feeding [14,62,63]. However, the diets of individuals from the same species can be dramatically different owing to different algal communities in their habitats. For example, in the Red Sea, large brown macroalgae are not a dominant part of the reef algal community. Rather, smaller brown, red and green turf algae occupy the role of macroalgae [45,64,65]. Nonetheless, these algae are fed upon by the same species who constitute grazers in the eastern Indo-Pacific Region. We suggest that this categorization should be inspired by terrestrial ecology and be based on the interaction of the mouth with the algae and/or the substrate, and the forces that the fish exert via mouth and body kinematics. Accordingly, grazers should be defined as fishes that scrape the substrate to remove the algae from its base, using body and fin kinematics to exert a push force towards the substrate and keep the mouth in close contact with it. Browsers should be defined as fishes that tear, shear or cut the algae somewhere along the thallus, using body and fin kinematics to exert a pull force on the algae without necessarily interacting with the substrate. According to this categorization species of the genus *Zebrasoma*, which are traditionally viewed as grazers, should be defined as browsers.

Previous research on the functional morphology of fishes that feed from the substrate has been largely based on morphological measurements, diet data or filming of feeding kinematics in a controlled laboratory environment. These studies identified numerous modifications of the feeding apparatus that facilitate forceful bites, algal tearing, efficient raking or large gape. Such modifications include the fusing of bones in the skull, resulting in reduced cranial mobility, and short and heavy jaws characterized by low mechanical advantage [30,31]. The evolution of the novel intra-mandibular joint within the lower jaw is considered an adaptation for

larger gape and the ability to close the mouth when the jaws are protruded [15,66,67]. Modified teeth are also evident in fish that feed from the substrate. In Scaridae and Tetraodontidae, fused beak-like teeth are used for scraping algae and corals or crushing the exoskeleton of armoured invertebrates [16,68], while in Acanthuridae serrated teeth are used for raking organic material from algal mats [14]. However, the functional morphology of the body and fins of fishes that feed from the substrate is far less clear. Our results show that bodily movements determine feeding performance in herbivorous fishes. Hence, the evolution of body and fin morphologies that facilitate the fish's ability to exert force on the substrate should be expected in herbivores and other substrate-biting fishes. For example, the laterally-compressed body morphology and the extended dorsal and anal fins of substrate-feeding reef fish families such as Acanthuridae, Chaetodontidae, Siganidae and Pomacanthidae could facilitate rapid sideways head motions ('head-flicks'), because the projected area of the body and extended fins increase the drag force, resisting the force of the head that accelerates laterally. Thus, this body shape may contribute to the species' ability to shear and tear attached prey. The elongated head and snout of these species may be an adaptation for generating faster lateral speed of the mouth, that could facilitate tearing of attached prey. Overall, our results demonstrate that body and fin morphology contribute to overcoming the functional demands of feeding from the substrate and that locomotory performance should not be relegated only to studies of habitat use and routine swimming.

Data accessibility. Data is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sbcc2fr49> [69].

Authors' contributions. T.P. carried out the field experiments and digitization of feeding videos. T.P. and R.H. initiated the research, analysed the data and wrote the manuscript. C.H.M. participated in planning the research, interpreting the results and writing the manuscript. A.R. designed and maintained the experimental system. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. This study was funded by U.S.-Israel Binational Science Foundation (grant no. 2016136).

Acknowledgements. We are indebted to L. Levy and R. Pickholtz, for help with data collection and digitization, A. Genin and Holzman laboratory members for insightful discussions, D. Churilov and M. Ohavia for technical help on the underwater system, and B. Shahar and M. Shpigel for help with developing the algal plate protocol.

References

- Higham TE, Hulsey CD, Ričan O, Carroll AM. 2007 Feeding with speed: prey capture evolution in cichlids. *J. Evol. Biol.* **20**, 70–78. (doi:10.1111/j.1420-9101.2006.01227.x)
- Higham TE. 2007 The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. *Integr. Comp. Biol.* **47**, 82–95. (doi:10.1093/icb/pcm021)
- Howland HC. 1974 Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333–350. (doi:10.1016/0022-5193(74)90202-1)
- Collar DC, Wainwright PC, Alfaro ME. 2008 Integrated diversification of locomotion and feeding in labrid fishes. *Biol. Lett.* **4**, 84–86. (doi:10.1098/rsbl.2007.0509)
- Sanford CPJ, Wainwright PC. 2002 Use of sonomicrometry demonstrates the link between prey capture kinematics and suction pressure in largemouth bass. *J. Exp. Biol.* **205**, 3445–3457.
- Losos JB. 1990 The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**, 1189–1203. (doi:10.1111/j.1558-5646.1990.tb05225.x)
- Hunter JP. 1998 Key innovations and the ecology of macroevolution. *Trends Ecol. Evol.* **13**, 31–36. (doi:10.1016/S0169-5347(97)01273-1)
- Webb PW. 1984 Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**, 107–120. (doi:10.1093/icb/24.1.107)
- Grant PR. 1999 *Ecology and evolution of Darwin's finches*. Princeton, NJ: Princeton University Press.
- Leisler B, Ley H-W, Habitat WH. 1989 Behaviour and morphology of *Acrocephalus* warblers: an integrated analysis. *Ornis Scand.* **20**, 181. (doi:10.2307/3676911)
- Spear LB, Ainley DG. 1998 Morphological differences relative to ecological segregation in petrels (family: Procellariidae) of the Southern Ocean and tropical Pacific. *Auk* **115**, 1017–1033. (doi:10.2307/4089519)

12. Gill FB, Wolf LL. 1978 Comparative foraging efficiencies of some montane sunbirds in Kenya. *Condor* **80**, 391–400. (doi:10.2307/1367189)
13. Paton DC, Collins BG. 1989 Bills and tongues of nectar-feeding birds: a review of morphology, function and performance, with intercontinental comparisons. *Austral. Ecol.* **14**, 473–506. (doi:10.1111/j.1442-9993.1989.tb01457.x)
14. Purcell SW, Bellwood DR. 1993 A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Environ. Biol. Fishes* **37**, 139–159. (doi:10.1007/BF00000589)
15. Ferry-Graham LA, Konow N. 2010 The intramandibular joint in *Girella*: a mechanism for increased force production? *J. Morphol.* **271**, 271–279.
16. Bellwood DR, Choat JH. 1990 A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ. Biol. Fishes* **28**, 189–214. (doi:10.1007/BF00751035)
17. Wainwright PC, Price SA. 2018 Innovation and diversity of the feeding mechanism in parrotfishes. In *Biology of parrotfishes* (eds AS Hoey, RM Bonaldo), pp. 26–41. Boca Raton, FL: CRC Press.
18. Fox R, Sunderland T, Hoey A, Bellwood D. 2009 Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. *Mar. Ecol. Prog. Ser.* **385**, 261–269. (doi:10.3354/meps08059)
19. Clements KD, German DP, Piché J, Tribollet A, Choat JH. 2016 Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. *Biol. J. Linn. Soc.* **120**, 729–751. (doi:10.1111/bij.12914)
20. Choat JH, Clements KD, Robbins W. 2002 The trophic status of herbivorous fishes on coral reefs. *Mar. Biol.* **140**, 613–623. (doi:10.1007/s00227-001-0715-3)
21. Choat JH, Robbins W, Clements KD. 2004 The trophic status of herbivorous fishes on coral reefs: II. Food processing modes and trophodynamics. *Mar. Biol.* **145**, 445–454. (doi:10.1007/s00227-004-1341-7)
22. Janis CM, Shoshitaishvili B, Kambic R, Figueirido B. 2012 On their knees: distal femur asymmetry in ungulates and its relationship to body size and locomotion. *J. Vertebr. Paleontol.* **32**, 433–445. (doi:10.1080/02724634.2012.635737)
23. Taylor C, Shkolnik A, Dmi'el R, Baharav D, Borut A. 1974 Running in cheetahs, gazelles, and goats: energy cost and limb configuration. *Am. J. Physiol.* **227**, 848–850. (doi:10.1152/ajplegacy.1974.227.4.848)
24. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008 A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci. USA* **105**, 19 052–19 059. (doi:10.1073/pnas.0800375105)
25. Shockey BJ. 2001 Specialized knee joints in some extinct, endemic, South American herbivores. *Acta Palaeontol. Pol.* **46**, 277–288.
26. Wainwright PC. 1996 Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology* **77**, 1336–1343. (doi:10.2307/2265531)
27. Wainwright PC, Bellwood DR. 2002 Ecomorphology of feeding in coral reef fishes. In *Coral reef fishes* (ed. PF Sale), pp. 33–55. San Diego, CA: Elsevier Academic Press.
28. Price SA, Holzman R, Near TJ, Wainwright PC. 2011 Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecol. Lett.* **14**, 462–469. (doi:10.1111/j.1461-0248.2011.01607.x)
29. Norton SF, Brainerd EL. 1993 Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11–29.
30. Westneat MW, Alfaro ME, Wainwright PC, Bellwood DR, Grubich JR, Fessler JL, Clements KD, Smith LL. 2005 Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. *Proc. R. Soc. B* **272**, 993–1000. (doi:10.1098/rspb.2004.3013)
31. Westneat MW. 2004 Evolution of levers and linkages in the feeding mechanisms of fishes. *Integr. Comp. Biol.* **44**, 378–389. (doi:10.1093/icb/44.5.378)
32. Tebbett SB, Goatley CHR, Bellwood DR. 2017 Clarifying functional roles: algal removal by the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus*. *Coral Reefs* **36**, 803–813. (doi:10.1007/s00338-017-1571-z)
33. Shadwick RE, Lauder GV. 2006 *Fish physiology: fish biomechanics*. San Diego, CA: Elsevier Academic Press.
34. Grobecker DB, Pietsch TW. 1979 High-speed cinematographic evidence for ultrafast feeding in antennariid anglerfishes. *Science* **205**, 1161–1162. (doi:10.1126/science.205.4411.1161)
35. Fulton CJ, Bellwood DR, Wainwright PC. 2001 The relationship between swimming ability and habitat use in wrasses (Labridae). *Mar. Biol.* **139**, 25–33. (doi:10.1007/s002270100565)
36. Colombo M, Indermaur A, Meyer BS, Salzburger W. 2016 Habitat use and its implications to functional morphology: niche partitioning and the evolution of locomotory morphology in Lake Tanganyikan cichlids (Perciformes: Cichlidae). *Biol. J. Linn. Soc.* **118**, 536–550. (doi:10.1111/bij.12754)
37. Walker JA, Westneat MW. 2002 Performance limits of labriform propulsion and correlates with fin shape and motion. *J. Exp. Biol.* **205**, 177–187.
38. Bejarano S, Jouffray JB, Chollet I, Allen R, Roff G, Marshall A, Steneck R, Ferse SC, Mumby PJ. 2017 The shape of success in a turbulent world: wave exposure filtering of coral reef herbivory. *Funct. Ecol.* **31**, 1312–1324. (doi:10.1111/1365-2435.12828)
39. Fulton CJ, Bellwood DR. 2004 Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. *Mar. Biol.* **144**, 429–437. (doi:10.1007/s00227-003-1216-3)
40. Wainwright PC, Bellwood DR, Westneat MW. 2002 Ecomorphology of locomotion in labrid fishes. *Environ. Biol. Fishes* **65**, 47–62. (doi:10.1023/A:1019671131001)
41. Webb PW. 1984 Form and function in fish swimming. *Sci. Am.* **251**, 72–83. (doi:10.1038/scientificamerican0784-72)
42. Rice AN, Cooper WJ, Westneat MW. 2008 Diversification of coordination patterns during feeding behaviour in cheilina wrasses. *Biol. J. Linn. Soc.* **93**, 289–308. (doi:10.1111/j.1095-8312.2007.00915.x)
43. Rice AN. 2005 Coordination of feeding, locomotor and visual systems in parrotfishes (Teleostei: Labridae). *J. Exp. Biol.* **208**, 3503–3518. (doi:10.1242/jeb.017779)
44. Brokovich E, Ayalon I, Einbinder S, Segev N, Shaked Y, Genin A, Kark S, Kiflawi M. 2010 Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. *Mar. Ecol. Prog. Ser.* **399**, 69–80. (doi:10.3354/meps08354)
45. Benayahu Y, Loya Y. 1977 Seasonal occurrence of benthic-algae communities and grazing regulation by sea urchins at the coral reefs of Eilat, Red Sea. In *Proceedings of the Third International Coral Reef Symposium, I. Biology*, pp. 383–389. Miami, FL: University of Miami.
46. Gillis GB, Lauder GV. 1994 Aquatic prey transport and the comparative kinematics of *Ambystoma tigrinum* feeding behaviors. *J. Exp. Biol.* **187**, 159–179.
47. Bellwood DR, Hughes TP, Folke C, Nyström M. 2004 Confronting the coral reef crisis. *Nature* **429**, 827–833. (doi:10.1038/nature02691)
48. Ogden JC, Lobel PS. 1978 The role of herbivorous fishes and urchins in coral reef communities. *Environ. Biol. Fishes* **3**, 49–63. (doi:10.1007/BF00006308)
49. Hughes TP. 1994 Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547–1551. (doi:10.1126/science.265.5178.1547)
50. Hughes TP *et al.* 2007 Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* **17**, 360–365. (doi:10.1016/j.cub.2006.12.049)
51. Edwards CB *et al.* 2014 Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proc. R. Soc. B* **281**, 20131835. (doi:10.1098/rspb.2013.1835)
52. Whitford MD, Freymiller GA, Higham TE, Clark RW. 2019 Determinants of predation success: how to survive an attack from a rattlesnake. *Funct. Ecol.* **33**, 1099–1109. (doi:10.1111/1365-2435.13318)
53. Day SW, Higham TE, Holzman R, Van Wassenbergh S. 2015 Morphology, kinematics, and dynamics: the mechanics of suction feeding in fishes. *Integr. Comp. Biol.* **55**, 21–35. (doi:10.1093/icb/ictv032)
54. Ferry-Graham LA, Lauder GV. 2001 Aquatic prey capture in ray-finned fishes: a century of progress and new directions. *J. Morphol.* **248**, 99–119. (doi:10.1002/jmor.1023)
55. Wainwright P, Carroll AM, Collar DC, Day SW, Higham TE, Holzman RA. 2007 Suction feeding mechanics, performance, and diversity in fishes. *Integr. Comp. Biol.* **47**, 96–106. (doi:10.1093/icb/icm032)
56. Wainwright PC, Day SW. 2007 The forces exerted by aquatic suction feeders on their prey. *J. R. Soc. Interface* **4**, 553–560. (doi:10.1098/rsif.2006.0197)

57. Holzman R, Collar DC, Mehta RS, Wainwright PC. 2012 An integrative modeling approach to elucidate suction-feeding performance. *J. Exp. Biol.* **215**, 1–13. (doi:10.1242/jeb.057851)
58. China V, Levy L, Liberzon A, Elmaliach T, Holzman R. 2017 Hydrodynamic regime determines the feeding success of larval fish through the modulation of strike kinematics. *Proc. R. Soc. B* **284**, 20170235. (doi:10.1098/rspb.2017.0235)
59. Day SW. 2005 Spatial and temporal patterns of water flow generated by suction-feeding bluegill sunfish *Lepomis macrochirus* resolved by particle image velocimetry. *J. Exp. Biol.* **208**, 2661–2671. (doi:10.1242/jeb.01708)
60. Sommerfeld N, Holzman R. 2019 The interaction between suction feeding performance and prey escape response determines feeding success in larval fish. *J. Exp. Biol.* **222**, jeb204834. (doi:10.1242/jeb.204834)
61. Olivier D, Parmentier E, Frédéric B. 2016 Insight into biting diversity to capture benthic prey in damselfishes (Pomacentridae). *Zool. Anz.* **264**, 47–55. (doi:10.1016/j.jcz.2016.07.006)
62. Green AL, Bellwood DR. 2009 *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific region*. Gland, Switzerland: IUCN.
63. Streit RP, Hoey AS, Bellwood DR. 2015 Feeding characteristics reveal functional distinctions among browsing herbivorous fishes on coral reefs. *Coral Reefs* **34**, 1037–1047. (doi:10.1007/s00338-015-1322-y)
64. Bahartan K, Zibdah M, Ahmed Y, Israel A, Brickner I, Abelson A. 2010 Macroalgae in the coral reefs of Eilat (Gulf of Aqaba, Red Sea) as a possible indicator of reef degradation. *Mar. Pollut. Bull.* **60**, 759–764. (doi:10.1016/j.marpolbul.2009.11.017)
65. Haas A, el-Zibdah M, Wild C. 2010 Seasonal monitoring of coral–algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. *Coral Reefs* **29**, 93–103. (doi:10.1007/s00338-009-0556-y)
66. Wainwright PC, Longo SJ. 2017 Functional innovations and the conquest of the oceans by acanthomorph fishes. *Curr. Biol.* **27**, R550–R557. (doi:10.1016/j.cub.2017.03.044)
67. Konow N, Bellwood DR. 2005 Prey-capture in *Pomacanthus semicirculatus* (Teleostei, Pomacanthidae): functional implications of intramandibular joints in marine angelfishes. *J. Exp. Biol.* **208**, 1421–1433. (doi:10.1242/jeb.01552)
68. Nanami A. 2016 Parrotfish grazing ability: interspecific differences in relation to jaw-lever mechanics and relative weight of adductor mandibulae on an Okinawan coral reef. *PeerJ* **4**, e2425. (doi:10.7717/peerj.2425)
69. Perevolotsky T, Martin CH, Rivlin A, Holzman R. 2020 Data from: Work that body: fin and body movements determine herbivore feeding performance within the natural reef environment. Dryad Digital Repository. (<https://doi.org/10.5061/dryad.sbcc2f49>)