Sixteen years of social and ecological dynamics reveal challenges and opportunities for adaptive management in sustaining the commons

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Efforts to confront the challenges of environmental change and uncertainty include attempts to adaptively manage social–ecological systems. However, critical questions remain about whether adaptive management can lead to sustainable outcomes for both ecosystems and society. Here, we make a contribution to these efforts by presenting a 16-y analysis of ecological outcomes and perceived livelihood impacts from adaptive coral reef management in Papua New Guinea. The adaptive management system we studied was a customary rotational fisheries closure system (akin to fallow agriculture), which helped to increase the biomass of reef fish and make fish less wary (more catchable) relative to openly fished areas. However, over time the amount of fish in openly fished reefs slowly declined. We found that, overall, resource users tended to have positive perceptions about this system, but there were negative perceptions when fishing was being prohibited. We also highlight some of the key traits of this adaptive management system, including 1) strong social cohesion, whereby leaders played a critical role in knowledge exchange; 2) high levels of compliance, which was facilitated via a "carrot-and-stick" approach that publicly rewarded good behavior and punished deviant behavior; and 3) high levels of participation by community actors.

social–ecological system | adaptive management | coral reef | customary management | fisheries

Adaptive management is thought to be a critical tool for helping to steer social–ecological systems through uncertainty and change (1–3). Often defined as an iterative process of changing management practices based on new experiences and insights, adaptive management continually tests, then refines both policies and actions (4, 5). Adaptive management is often, but not always, part of multiscale governance arrangements, including adaptive comanagement [a flexible, but locally tailored system of management supported by organizations at larger scales (6)] and adaptive governance [the interactions of actors, networks, institutions, and organizations that emerge as social–ecological systems are steered toward a desired state (7)]. Indeed, adaptive management is practiced in a wide range of contexts ranging from formal processes of large-scale ecosystem-based management, e.g., the Great Barrier Reef and the Everglades (2, 4, 8), to informal long-enduring customary management and traditional ecological knowledge systems (9, 10), e.g., shifting cultivation practices (10), nomadic herding (11), and rotational fisheries closures (12, 13), the latter of which is the focus of this present article.

Despite the widespread use of adaptive management, critical questions remain about whether and how it may lead to sustainable outcomes for both societies and ecosystems (14). To date, many studies of adaptive management outcomes have tended to suffer from 2 key shortcomings. First, many studies focus on either social or ecological outcomes (3, 8, 15). However, there may be critical trade-offs between social and ecological domains (16, 17). Second, few empirical studies have quantitatively examined both social and ecological outcomes through multiple phases of adaptive management (14). This is crucial because the dynamic nature of adaptive management necessarily implies that there are likely to be ebbs and flows of specific outcomes.

In addition to understanding the outcomes produced by adaptive management, it is also crucial to identify key social, economic, and institutional traits that may enable adaptive management. Doing so can help to elucidate and avoid barriers to implementing adaptive management at other locations and scales (7). Research on both collective action and adaptive management have emphasized a few key enabling conditions, including the following: property rights systems that allow the exclusion of "outsiders" at

Significance

Coral reefs provide ecosystem goods and services for millions of people, but reef health is declining worldwide and current approaches have failed to prevent losses. Adaptive approaches that reflect local social, economic, and cultural conditions are required. We conducted social and ecological research across 5 time intervals over 16 y to study the key traits of a long-enduring customary adaptive reef management system in Papua New Guinea. Resource users identified high levels of compliance, strong leadership and social cohesion, and participatory decision making among community members as key traits of a rotational fisheries closure system, which increases fish biomass and makes fish less wary (hence more catchable), relative to openly fished areas.

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relatively low costs; flexible and polycentric institutions that facilitate participation and experimentation; strong social networks that support dialogue, learning, and information sharing; monitoring of resources; and users support for enforcement (7, 18, 19). However, many of these key traits have been derived from theory and/or comparative studies, rather than from the perspective of resource users themselves. Understanding local perspectives helps illuminate social, cultural, political, and economic factors critical to the management success in a given context (20), gauge the legitimacy and acceptability of governance (21), and ultimately ensure that management is not culturally inappropriate or inequitable (22). Better understanding emically derived (i.e., from the perspective of people in local communities) key traits, particularly those in long-enduring customary-based adaptive management systems, may therefore help to shed light on aspects of patterns, practices, and processes that may not be immediately apparent from the perspective of outsiders.

Here, we make a contribution to the literature by presenting a 16-y analysis of ecological outcomes, perceived livelihood impacts, and key traits of a long-enduring customary adaptive coral reef management system (23). Specifically, we ask, "How do key ecological outcomes and users' perceptions of adaptive management change over time?" and "What do resource users perceive to be the key traits of this long-enduring adaptive management system?" In exploring these questions, we examine whether ecological integrity is maintained at the expense of community values.

We conducted social and ecological research across 5 time intervals on a complex of coral reefs and associated coastal communities in Papua New Guinea (24). Our approach first explores the ecological outcomes from an adaptive rotational reef closure system (akin to fallow agriculture) (Box 1; Figs. 1 and 2), and how resource users perceive this system impacts their livelihoods. To explore the ecological outcomes of the adaptive management system, we used underwater visual census of reef fish to estimate 1) the biomass of reef fish (a metric used to assess the state of the fish stocks) over time; and 2) how the flight initiation distance (FID) behavior of 6 key reef fish species changes as reefs are opened and closed (*Methods* and Table 1). FID is a key behavioral metric related to fish catchability and a key rationale behind the adaptive rotational closure system used by these communities is that closures alter fish behavior in ways that make fishing easier (25, 26). Specifically, exposure to fishing activities makes fish more "afraid" of people, resulting in flighty behavior that makes it difficult to get close to fish (25). These flightier fish are perceived to be much harder to catch, particularly with spearguns (13, 25). It is noteworthy that the complex of reefs in front of these communities (Fig. 1*C*) was identified in ref. 23 as a bright spot, defined as reefs that have more fish biomass than expected, given the social and environmental conditions they are exposed to. We used household surveys to explore resource users' perceptions of whether and how these customary management practices impacted their livelihoods. We then use qualitative and quantitative social science research to identify and explore what local community members believe are 3 key traits of this long-enduring adaptive management system: 1) compliance; 2) leadership and social cohesion; and 3) participatory decision making among community members.

Results

Ecological Outcome 1: Fish Biomass. Our reef surveys revealed that, overall, reefs closed to fishing had more than double the mean total biomass (654.6 kg/ha $\pm$ 108.4 SE) of reefs open to fishing (252.6 kg/ha $\pm$ 17.2 SE) (Fig. 3; $P \leq 0.01$). Moreover, certain types of fishes thought to play important functional roles in reef ecosystems (excavators/scrapers, grazers, microinvertivores, and macroinvertivores) exhibited significantly higher biomass when closures were in place (Fig. 3 *B*, *C*, *E*, and *F* and *SI Appendix*, Table S2). Due to a high prevalence of zero abundance of select families in the transect data, we used roving surveys to examine browsers and piscivores. We found the biomass of browsers and piscivores were also higher when closures were in place, but this difference was only significant at $P < 0.1$ (Fig. 3 *D* and *H*). Although there was higher fish biomass inside closures relative to openly fished areas throughout the study, the absolute amount of fish biomass showed signs of decline over time, despite increasing coral cover (Fig. 3*A*). Indeed, biomass in openly fished reefs in 2017 [158 (13.8 SE) kg/ha] was less than a third of estimated biomass in 2001 [517 (124.4 SE) kg/ha].

Ecological Outcome 2: Changing Fish Behavior. We found that FID was higher (i.e., fish were more wary) when reefs were open to fishing compared to when they were closed (Fig. 4 and *SI Appendix*, Table S3). Specifically, in 2009, Wadau (when reefs were open to fishing) estimates of FID were 128 cm higher than in 2012, when the same reefs were closed to fishing ($t = -11.3$, df = 372, $P < 0.001$). Alternatively, we observed the opposite trend in FID when reefs closed to fishing were subsequently opened. In Muluk, estimates of FID in 2009 when the reef was closed were 84 cm lower than those found for fishes observed in 2012, when the reef was open to fishing ($t = -8.4$, df = 476, $P < 0.001$; *SI Appendix*, Table S3).

Perceived Impacts of Customary Management on Resource Users' Livelihoods. Our quantitative survey revealed that both villages perceived the closure system as beneficial to people's livelihoods,

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Box 1.

Both villages employ a rotational closure system, whereby reef-associated fishing grounds are periodically closed to all fishing activity (heretofore referred to as "closure"; *SI Appendix*). When closed, all fishing and gleaning on a specific section of reef is prohibited. Men may still fish in deeper water beyond the reef crest (Fig. 1*C*) (women are traditionally excluded from this deep-water fishing). The rotational closures are founded on a strong customary marine tenure system, whereby clans have the right to exclude both clan and nonclan members from specific fishing grounds. Since 2001, the reefs in each village underwent cycles of rotational closure, which we surveyed 5 times (Table 1). The closures are adaptive in that the specific location, size, and duration of the closure can vary (i.e., the closure size can range from a specific portion of the reef to the entire community's reefs, and can last up to 9 y). The ending of a closure is often marked by a large harvesting event and an accompanying celebratory feast (Fig. 2 *A*–*C*). For example, in 2017, a reef opening culminated in a ceremony attended by around 300 people from Muluk and surrounding communities. Clan leaders, the local pastor, and visiting political candidates gave speeches about conserving the reef, and community members and visitors were gifted fish (Fig. 2*C*), which were caught in the week preceding the ceremony (Fig. 2*A*) and smoked for preservation (Fig. 2*B*). Both villages also employ a traditional bamboo harpoon method of fishing (called "*bom bom*"; Fig. 2*D*) used at night. Fishers use light (traditionally fire, but now a lamp; Fig. 2*D*) to attract flying fish (family: Exocoetidae) and needle fish (family: Belonidae) that are then speared. To use this method, fishers not only adhere to a strict set of customary laws but must also first undergo an initiation process. The *bom bom* fishing method, the rotational closure practice, and the customary marine tenure system that underpin them have been passed down through generations, with living memory of them predating World War II.

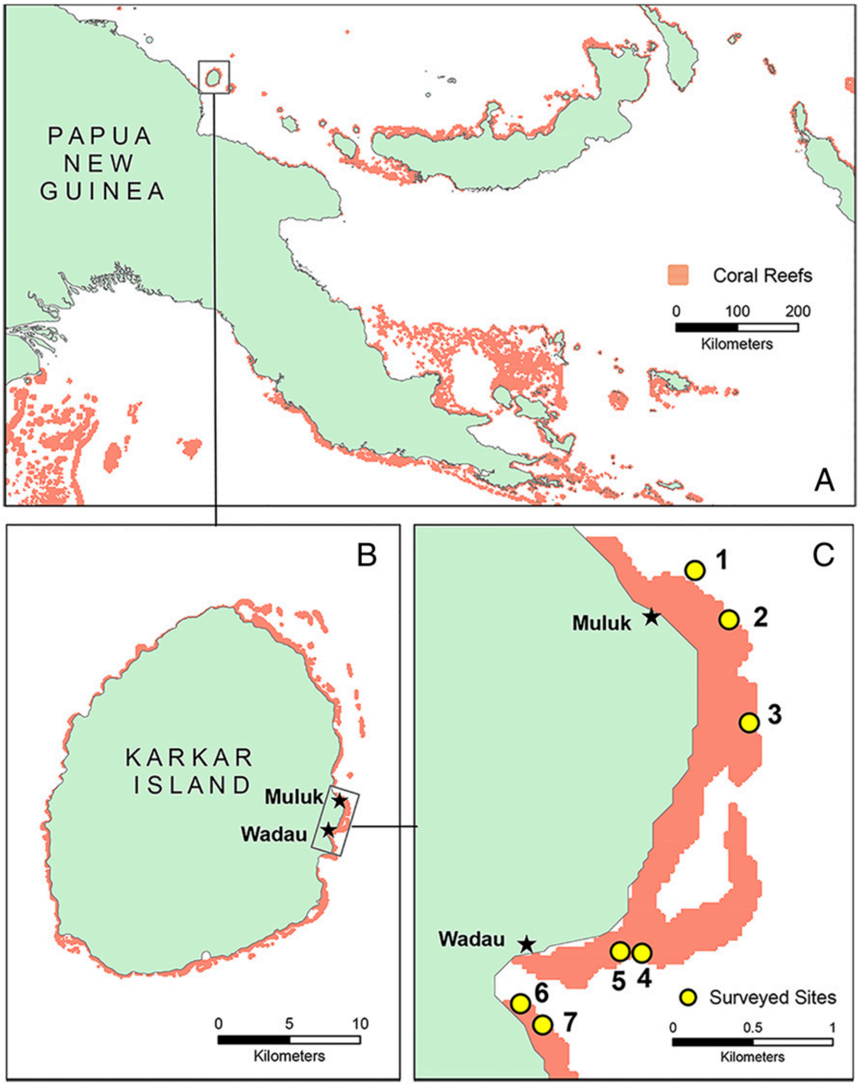

Fig. 1. (*A–C*) Map of study sites. Points 1 to 7 in *C* are the locations where ecological surveys were periodically conducted between 2001 and 2017 (*Methods*).

even though the closure limited fishing opportunities. Specifically, a strong majority of resource users (60 to 85%, depending on whether reefs were closed or open to fishing at the time of data collection) perceived the closure system as beneficial to their livelihoods (Fig. 5). Only a small minority (<24%, depending on the year and location) of respondents perceived the closure system to be detrimental to their livelihoods, and this was only when closures were active (Fig. 5). The prevalence of negative opinions was significantly related to closed status (Fisher's test, $P < 0.02$).

Our qualitative interviews helped to elucidate 3 keys reasons why people felt they benefited from the closure system (*SI Appendix*, Table S4). First, people perceived that good fortune befalls people who follow customary laws such as the closure (and vice versa—harm will come to people who break customary rules). Customary laws dictate certain practices and rules around fishing (including abstaining from eating certain fruit and abstaining from fishing while one's wife is menstruating). For instance, one clan leader explained that "you must follow [the customary law], and you will see that you have plenty of fish and plenty of pigs and plenty of whatever you need. If you don't follow the law, you will lose all these things. This custom, it's so important here...." Thus, benefiting from the reef is seen as inextricable from following the customary laws. Second, customs are perceived to create important connections among people, to ancestors, and to place, which helped form identity. For example, an interviewee mentioned: "It's something good that we have here; the way that we help other people, and work together and participate in big customary events in the community. Other places don't have this. Other places have gradually lost these ways." Indeed, part of this identity stems from the prestige awarded from being able to host a feast and gift food to visitors (Fig. 2*C*). Finally, respondents perceived that the closure would make fishing easier for men and women in the community, in part through changing fish behavior (making fish less wary) and in part through increasing the amount of fish. For example, one interviewee noted "by closing the sea, we let it rest. No one can go into the sea to disturb the reef or disturb the fish. No one can go and frighten the fish in the reef. It'll be easier in the future... all the fish will grow up and then men and women from the community will find it easier to catch fish, even close to the beach, and bring them home to eat."

Key Trait 1. Compliance. Our quantitative surveys found that compliance rates were generally high. For example, in 2001, 70% of respondents noted that closures were fully or mostly complied with, and this proportion increased to 84% in 2016. Only 8% of Muluk respondents in 2016 reported seeing someone poach within

Fig. 2. Customary fishing practices. The ending of reef closures is often marked by community harvests of the reef. Harvests (*A*) are dried and smoked (*B*) in preparation for a feast (*C*). (*D*) Reenactment of the traditional harpoon fishing method known as *bom bom*.

closed reefs in the past 12 mo. Interviews with clan leaders suggested that social norms and sanctioning processes play a large role in sustaining high compliance levels (*SI Appendix*, Table S5). A "carrot-and-stick" approach is used. On the stick side, clan chiefs single out and penalize rule breakers, thereby increasing social pressure to comply. For example, an interviewee in Muluk noted: "If [a youth] is disobedient, then we'll bring him here to talk, and to follow the law of custom. Custom is the same as law, the law of the village. . .you can't flaunt it. You can't mess with it." On the carrot side, respectful behavior is rewarded. Every few years, clan leaders, parents, and elders select well-behaved, strong, and respectful young men to undergo the prestigious fishing initiation ritual that provides the "license" to fish at night using the *bom bom* method described above (Fig. 2*D*).

Key Trait 2: Participatory Decision Making among Community Members. Both Wadau and Muluk have regular deliberative and adaptive processes in place to make decisions, including those about the closure. Each community holds a weekly meeting to discuss community issues, and clan meetings when necessary. Several interview respondents considered this deliberative decision making a key part of ensuring customary practices remained strong (*SI Appendix*, Table S6). For instance, one interviewee emphasized that "all of the leaders meet, and argue about [issues], and make sure the customs stay strong." Although clan leaders are ultimately responsible for decisions, people in both communities are highly involved in decision making. Between 2001 and 2016, 95% of respondents reported being involved in community decisions (61% reported being actively involved whereby they spoke and shared ideas at community meetings, and 34% reported being passively involved, whereby they attended but did not contribute to meetings). These figures were broadly consistent across years with active involvement ranging from 58 to 73% of respondents, passive involvement ranging from 26 to 42%, and no involvement ranging from 0 to 10%, depending on the year. Likewise, between 2009 and 2016, 92% of respondents reported being involved in decision making specifically related to the reef (55% actively involved and 37% passively; decision making specific to reef not asked in 2001).

Decisions about when to close or open reefs to fishing activities were reportedly made based on social and ecological feedbacks (*SI Appendix*). One interviewee noted: "If the leader sees that the number of fish has gone down and we're ruining the sea, then the leader will say, it's closed. Ok. If the leader says, there are plenty of fish, now we can catch fish." In addition, ending of closures can also be timed to provide for social gatherings within or between clans (i.e., opening reef sections to provide food for a feast following the death of a community leader, or for Christmas), or when community members feel the reef has been closed long enough. In Muluk, each clan also deliberates on the fishing rules within their reef section before it is opened to fishing activities. In 2017, all 3 clans banned night spear-fishing, limited the use of nets, and banned derris root (a poison that stuns fish). Rules were passed by consensus among clan members.

Key Trait 3. Leadership and Social Cohesion. The third key trait identified by our qualitative interviews centered around the integration of leadership and social cohesion (*SI Appendix*, Table S7). Strong and respected leadership was considered an essential aspect of Muluk and Wadau. In addition, respondents also highlighted a strong sense of social cohesion. For example, one respondent noted "So, you'll see that our community isn't divided. We are all together as one whole community. If you go to other communities you'll see, over there is a little part of the village, another is over there, and over there, it's all broken up. So it's hard to communicate and bring people together to talk and come to common understandings. But not here; here, our community is intact, and we must stay like this." Furthermore, respondents also identified youth–elder ties as a critical part of their social cohesion.

To quantitatively examine leadership and social cohesion, including youth–elder ties, we conducted an analysis of fisheries-related knowledge exchange networks using social network analysis methods in Muluk in 2016 (Fig. 6). We found that traditional leaders received significantly more knowledge seeking ties (*SI Appendix*, Table S8), demonstrating that many people in the community consider leaders important sources of fisheries-related knowledge and advice. Our exponential random graph model (ERGM) did not reveal any significant effects of age on the formation of directed knowledge-sharing ties. However, when we examined patterns of knowledge exchange across age cohorts (elders, middle-aged, and youth), we found that elders had a much higher level of between cohort ties (i.e., ties to middle-aged and youth) than within cohort ties (E–I index of 0.667; *Methods* and *SI Appendix*, Table S9). By comparison, youth and middle-aged fishers tended to form slightly more within cohort ties (*SI Appendix*, Table S9). Elders also had over twice as many incoming ties (indegree) as outgoing ties (outdegree). Combined, these results suggest that the knowledge exchange networks are loosely clustered around traditional leaders, yet elders are also seen as important sources of information and advice and play a key role in knowledge communication across generations.

Considering the knowledge exchange network as a whole, we found evidence of a very open, nonhierarchical social structure where people are not necessarily bound by any specific group membership and thus have more or less equal opportunities to engage in knowledge exchange with all others in the community (Fig. 6). Importantly, leaders are more or less evenly distributed throughout the network (rather than clustered in a center "core"), and they do not preferentially interact with each other (i.e., there is no homophily among

Table 1. Reef sites (corresponding to Fig. 1*C*) and closure status by year of survey

Site	Community	2001	2009	2012	2016	2017
1	Muluk	Closed	X	Open	Closed	Open
2	Muluk	Closed	Closed	Open	Closed	Open
3	Muluk	Closed	Closed	Open	Closed	Open
4	Wadau	Open	Open	Closed	Open	Open
5	Wadau	Open	Open	Closed	Open	Open
6	Wadau	Open	X	Open	Open	Open
7	Wadau	Open	X	X	Open	Open
Closure duration		1 y	9 y*	2 y	3 y	NA

X, not surveyed in a specific year.
*Open for ∼2 wk during this 9-y period.

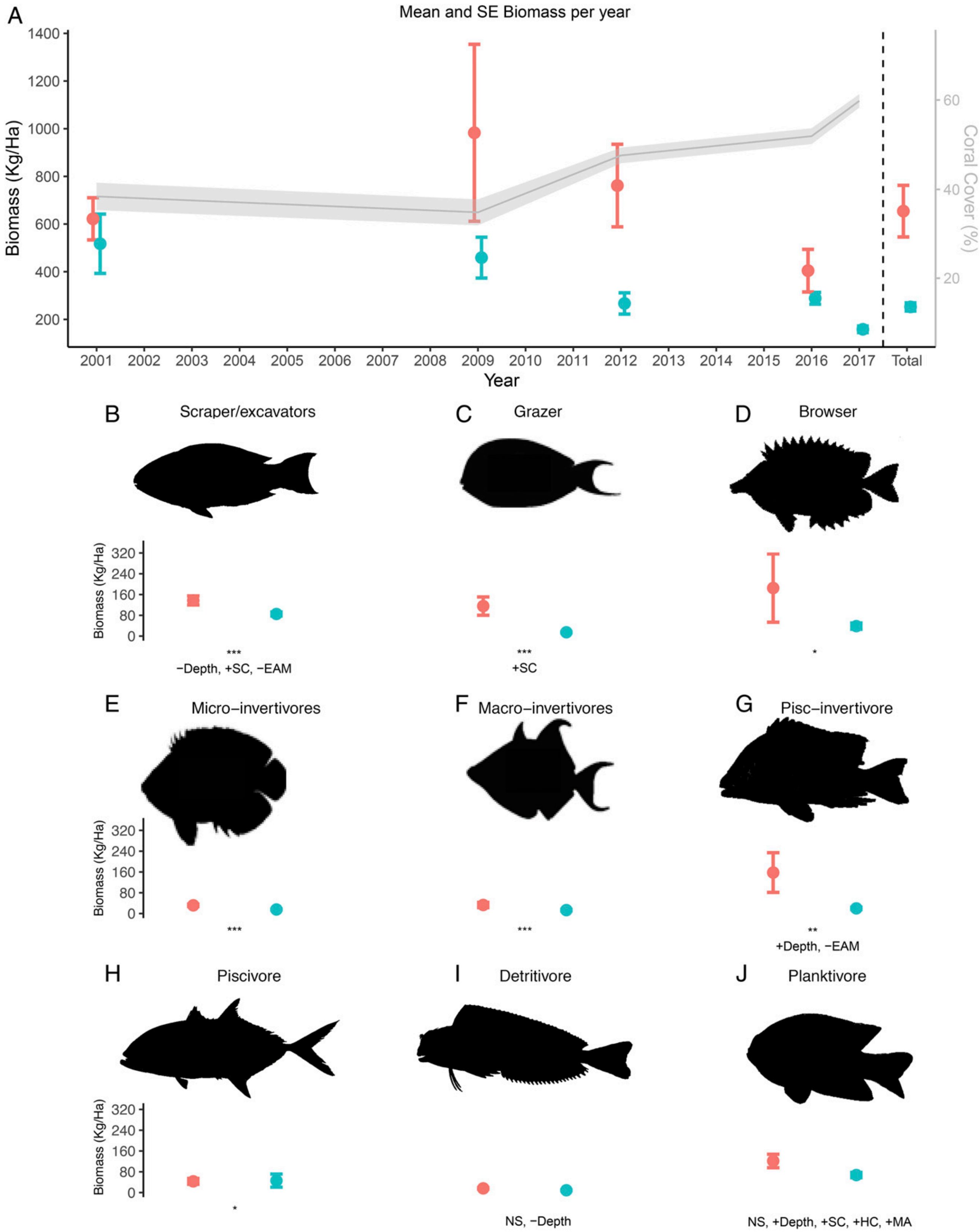

Fig. 3. Reef fish biomass (mean + SE) within (red) and outside (green) customary closures. (*A*) Reef fish biomass of 6 select families (Acanthridae, Scaridae, Siganidae, Lutjanidae, Haemulidae, Serranidae: *y* axis) in closed (red) and open (blue) areas, plus coral cover (gray line, *z* axis) for 2001, 2009, 2012, 2016, 2017, and total of all years. (*B*, *C*, *E*–*G*, *I*, and *J*) Aggregate differences in functional group (feeding guild) biomass between open and closed reefs across years from 2009 to 2017. Asterisks indicate level of significant difference between biomass estimates within each group (*$P < 0.10$; **$P < 0.05$; ***$P < 0.01$), with the relationship to key biotic (benthic community taxa) and abiotic factors listed below each graph. EAM, epilithic algal matrix; HC, hard coral; MA, macro algae; SC, structural complexity (−, negative relationship; +, positive relationship); NS, nonsignificant. Biomass estimates of browsers (*D*) and piscivores (*H*) are from timed swims in 2016 only, and these models do not include other covariates.

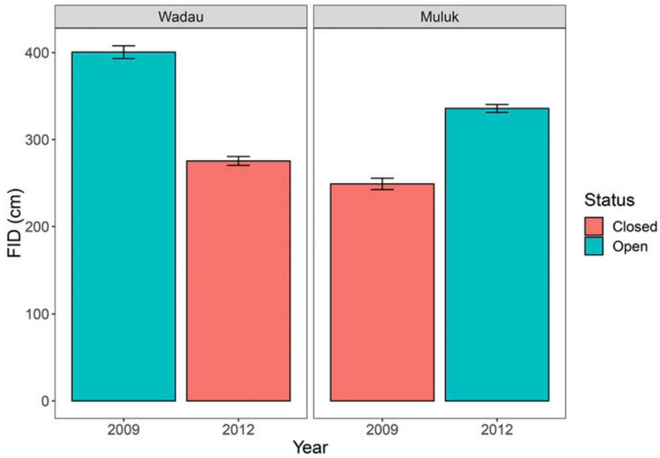

Fig. 4. Model predicted fish flight initiation distance (FID) plus SE. From open to closed to fishing (Wadau 2009 to 2012) and from closed to open (Muluk 2009 to 2012). The linear mixed-effect model controlled for differences in species composition among sites.

leaders). In addition, there is no substantial tendency toward network closure (i.e., clustering) or centralization (which can be indicative of a hierarchical network structure). There is also no significant tendency for people to preferentially share knowledge within their clan (homophily). Moreover, members of one clan are not more or less active in the network than members of other clans.

Discussion

Our detailed social–ecological investigation revealed 2 key findings; first, the adaptive management of reef resources appears to be enabled by social and cultural processes that may have important lessons for collective governance of common pool resources in other locations. In particular, key aspects of the customary rotational closure system appear to harness both social influence levers and cognitive biases to foster compliance and the acceptability of management (27, 28). Existing research demonstrates that people's behavior is profoundly influenced by their desire to maintain prestige, conformity, and reciprocity, and these desires are often based on social norms about acceptable behavior (27). In Muluk and Wadau, both the public sanctioning and initiation ritual reinforce injunctive social norms (i.e., what is "the right thing to do") around compliance (29). The public sanctioning identified by community members as part of their compliance mechanisms (*SI Appendix*, Table S6) likely invokes a sense of shame for the rule breaker by publicly calling out bad behavior. Alternatively, being selected for the initiation ritual to be able to access the *bom bom* fishery provides positive incentives for following the rules, reinforcing the norms around compliance. This type of carrot-and-stick approach to compliance that targets social norms can likely help complement compliance efforts in other locations (29).

The existence of only positive or neutral perceptions about the closure when it was inactive, but some negative perceptions when it was active, can potentially be explained by a variation of the "peak-end heuristic" (28). Peak-end is a phenomenon in which there is a distinction between what people experience and what they remember, with people remembering only the peak (most intense part) and the end of an experience (whether positive or negative), regardless of length (28). While the closure was in place (and people could not fish on the reef), some people had a negative perception of it (Fig. 3). However, the end of the closure coincides with changes in fish behavior that have been shown to improve fish catch (26) and an event that brings prestige to the community, which may result in people having a more positive view of the closure when asked about it when the reef is open to fishing. Thus, the long-term support for these customary closures may in part be derived from leveraging cognitive biases in community members—a concept that has potential applications for resource management in other locations (27). More detailed longitudinal data would be needed to confirm this potential explanation for the pattern we observed; but regardless, the lack of negative perceptions after a closure may mean that people are likely more agreeable to initiating the next closure cycle.

The adaptive management system was also characterized by strong leadership and social cohesion, high levels of participation in deliberative and adaptive decision making by community members, and customary marine tenure property rights that serve as a foundation for developing and enforcing rules. Although leadership and social cohesion are known to be important for successful resource management outcomes, they are often grouped together with other important social drivers, particularly social cohesion, which tends to be discussed under the broad umbrella term "social capital" (e.g., ref. 30). This grouping skews our understanding of how these two attributes interact to facilitate successful outcomes. Here, our emic exploration of this issue helps to shed light on potential underlying processes. Despite a customary clan-based social system, there is a strong sense of community that transcends clan membership and age cohorts and involves shared views, perceptions, and norms. This strong sense of community (i.e., social cohesion) is in part upheld by proactive leaders and elders who garner a high level of respect from the community (31). The deliberative and adaptive processes highlighted in Muluk and Wadau likely also contribute to strong social cohesion among the community, because these processes suggest high levels of community participation (32) and procedural justice (33), which can foster perceived legitimacy and acceptability of management. Although the specific decision-making arenas used in Muluk and Wadau (weekly community meetings) might not be appropriate or applicable in other places, the broader practice of deliberative and adaptive management certainly is. Last, customary practices such as *bom bom* fishing and the rotational closure system depend on the cultural and legal norm of customary marine tenure, which enables the exclusion of "outsiders" from certain fishing practices and grounds (in this case, tenure is decided at the clan level). This tenure system provides a rights-based foundation critical to the development and enforcement of locally appropriate rules. In many parts of the world, rights-based systems of fisheries management are proliferating, with varying degrees of success (34, 35). Further understanding the establishment, transmission, and maintenance of norms in rights-based systems may elucidate reasons for failures or successes (36).

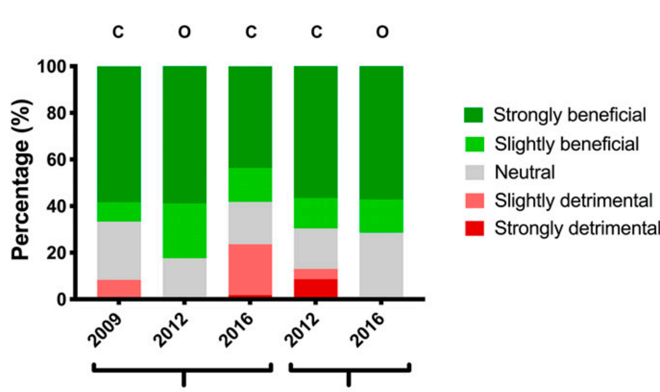

Fig. 5. Percentage of respondents who perceived beneficial and detrimental impacts of the periodic closure system to their livelihood. C, closure in place; O, open to fishing.

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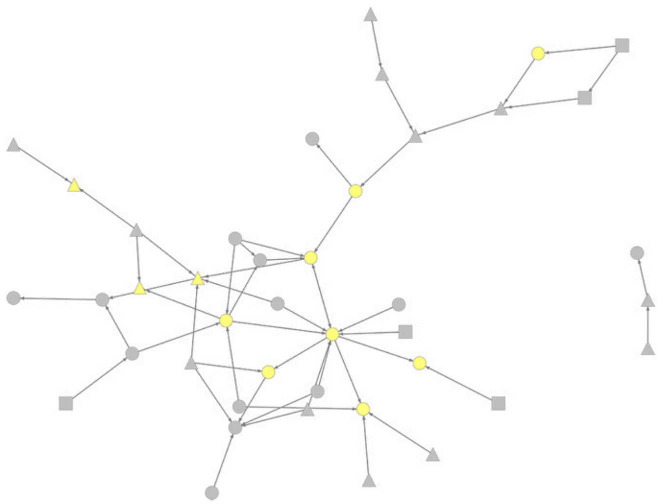

Fig. 6. Fisheries-related knowledge sharing network among respondent fishers in Muluk (n = 41) in 2016. The arrows point to sources of information and advice. Node shapes represent different clans; traditional leaders are shaded in yellow. An ERGM of this directed network indicates a very open (i.e., nonclustered) and nonhierarchical social structure loosely organized around traditional leaders (*SI Appendix*, Table S8). Results also indicate that clan membership does not significantly influence the formation of knowledge-sharing ties.

Ecological Outcomes. The second key finding is that, sadly, despite the well-complied-with adaptive management system, fish biomass appears to be declining over time. When customary rotational closures in Muluk and Wadau were in place, the overall biomass of reef fish tended to be more than double that of open reefs (Fig. 5)—an outcome that contributed to this location being identified as a bright spot (23). However, are the ecological benefits of this closure enough to sustain key ecological processes?

On one hand, this rotational closure system was associated with considerable ecological success. There was significantly higher biomass of select functional fish groups that are thought to aid in sustaining healthy, coral-dominated, tropical reef ecosystems (*SI Appendix*, Table S2). These groups include, for example, grazers and scrapers/excavators, which are vital for removing epilithic algal matrix (EAM) and sediment, creating open space for coral settlement (37, 38), and transferring energy and nutrients to other consumers in the food web (39). Thus, while the closures are in place, it is possible that certain functions are bolstered. Additionally, in stark contrast to the global trend of declining coral cover (40), overall coral cover at these sites increased substantially over the 16-y study period. This suggests that other environmental disturbances such as coral bleaching or crown of thorns starfish have not severely impacted the reefs here. However, on the other hand, the overall amount of biomass in reefs open to fishing has eroded dramatically over the 16-y study period. Indeed, the biomass levels in 2017 (158 kg/ha) were approaching the reference point of a collapsed reef fishery (10% of unfished biomass or ~100 kg/ha, given average conditions) identified in ref. 41. While the fish biomass in the closures was at or above the levels thought to maintain reefs above key ecological thresholds (42), the biomass in the fished areas was below these thresholds, especially in more recent years. This finding suggests that the rotational closure system may provide a temporary boost to biomass but may not be enough to stem the overall impacts of overfishing. It is noteworthy that, in 2017, we specifically conducted our fish and benthic surveys as close as possible following the end of the closure (and associated large harvesting event) to try and capture the low baseline (Fig. 2). It is possible that the biomass will build from this low baseline closer to the long-term average (Fig. 2*A*).

Social–Ecological Trade-Offs: Balancing Ecological Integrity and Community Values. A critical question is why a system that has been in place for generations has recently resulted in the erosion of reef fish biomass to a concerning level? Plausible explanations include the substantial increase in human population (the population of Muluk more than doubled between 2001 and 2016). This increase in population may increase harvest intensity on the relatively small reef area (~92 ha) (13) not only during the opening harvest (more people to feed at a feast and more fishers), but also throughout the open cycle as more people access fishery resources, and may also increase the number of harvest events (e.g., more marriages, community events). Importantly, closure duration and harvest intensity are malleable aspects of this management system that can be adjusted by decision makers and community members resulting in dynamic and changing timing of closure cycles (Table 1), and it is likely that the duration of closure relative to harvest intensity is decreasing over time, although details about historical closure durations were not known. Closure duration can have big impacts on the ecological efficacy of nonpermanent closure systems (43–45), and it was clear that the highest biomass estimates we recorded were from the period when the closure had been implemented the longest (~9 y). With the increase in human population, and potentially increases of harvesting events (e.g., increased numbers of marriages, school fees, etc.), changing closure duration may also interact with one of the reasons for implementing closures: the change in fish behavior. Our temporal analysis building on previous inside–outside comparisons (25) demonstrates how fish flightiness decreases as reefs are closed to fishing, and increases as reefs are open to fishing. Fish behavioral change can be more sensitive than biomass to temporally short closures (26, 46), and increased ease of catching fish may mask declines in fish biomass between rotational openings (i.e., a form of hyperstability where catches appear stable despite declining stocks). It is worth noting that although wariness is likely to affect catch rates, it is unlikely to affect biomass estimates because the maximum flight distance is well within the distance at which fish are counted (in other words, one has to get much closer to shoot a fish than to count it) (25). The sustainability of the resource base may therefore fluctuate with changes in fish behavior. However, the very malleability of the system can allow decision makers and community members to adjust closure cycles to allow a rebuilding of their fish stocks.

The finding that biomass is declining over time is particularly relevant given that this location was identified as a "bright spot"—one of 15 sites in a global study of ~2,600 coral reefs that had fish biomass levels >2 SDs higher than expected, given the social and environmental conditions present. Our finding that ecological conditions have declined after repeated harvesting is not necessarily surprising, but the implications are that bright spots can be ephemeral with changes to management. This not only means that bright spots can dim with changes to management, but that dark spots could brighten. An important area of future research is systematically examining the bright spots of recovery dynamics (i.e., are there places that are recovering better than expected given their conditions or not declining as fast as expected, given their conditions). One rationale for exploring both social and ecological dynamics, was to investigate possible trade-offs between whether this site was bright ecologically, but dark socially (i.e., that the positive ecological state identified in ref. 23 could have been a result of processes that exclude people from accessing resources, negatively affecting their livelihoods). Given the extremely positive views toward the management system's effect on people's livelihoods, it seems unlikely that this spot is socially dark. If anything, the system may be trending toward the opposite way; where people perceived a range of benefits from the management system (socially bright), but the resource is dwindling over time (ecologically dimming). Nonetheless, despite diminishing fish stocks, people perceived a range of benefits from the closure system, which will likely facilitate continued and active participation by community members in and acceptance of resource management in the future. The harvest ceremony after the opening not only provides the community with direct benefits, such as improved fishing opportunities and food for a feast, but also prestige from being able to gift fish to other communities. Indeed, deliberately including positive experiences (like celebratory harvests) in other resource management systems could potentially shape positive perceptions. A critical challenge will be adapting the management so it can continue to generate key benefits without eroding the ecological system upon which they are founded. Recent modeling work highlights that optimal benefits from periodic closures occur when only a single pulse harvesting event is permitted (47).

Critiques and Caveats. Our investigation was an important first step in exploring the social and ecological dynamics associated with local adaptive reef management, but has several key shortcomings that may limit the inferences and transferability of the key findings. First, although our study represents one of the longest-term analyses of a coral reef social–ecological system to date, funding and fieldwork realities meant that the sampling intervals were uneven and not all questions were asked at each sampling interval.

Second, our methodology did not allow us to make causal inferences about the conditions we identified. Our emic approach was designed to explore key social and ecological phenomena as identified from the perspective of people in local communities, rather than demonstrate causality. Future studies employing experimental designs will be required to test how the key traits identified in this paper lead to ecological and social outcomes (including income, equity, food security, and well-being; ref. 48).

Third, because this is a single case study of how a rotational reef closure system provided benefits in Muluk and Wadau, the transferability of this specific form of management to other social–ecological settings may be limited (49). Muluk and Wadau are small communities, where transgressors can be easily identified and punished by leveraging social norms such as shame and ostracism. However, larger, more anonymous communities might struggle to implement these specific strategies (50). Likewise, people's livelihoods in Muluk and Wadau tended to primarily focus on agriculture, rather than fisheries (13). Communities with higher dependence on fisheries may not have the flexibility to close their fishing grounds for extended periods of time without impacting their primary livelihood activity. Thus, the specific type of rotational closure employed here may not be desirable in other locations.

Last, our study was primarily focused on the local dynamics and did not delve deeply into how the larger-scale context (i.e., cross-scale interactions, teleconnections, distal drivers of change) shapes this coral reef social–ecological system (23, 51). For example, livelihoods and resource use patterns on Karkar are also likely shaped in part by teleconnections with distant places through international markets for agricultural cash crops (copra, cocoa) and marine products (shark fins, beche-de-mer) (52). Land use practices and resource harvesting may respond not only to fluctuating international market prices but also to government policies that attempt to mitigate the negative environmental effects of these teleconnections (such as a countrywide moratorium on beche-de-mer) (53).

Conclusion

Despite these caveats, our 16-y social–ecological analysis makes a contribution to the literature by highlighting 4 key social–ecological features that may have relevance to other locations: 1) Management practices were built on a strong customary foundation, which included a marine tenure system whereby "outsiders" could be excluded; these customary and right-based foundations allow management practices to be tailored to the local context and adaptive to changing conditions; 2) compliance was managed using a carrot-and-stick approach that publicly rewarded good behavior and punished deviant behavior (29); this approach essentially leveraged people's desire to align with social norms, an area of increasing interest in conservation (50, 54); 3) the long-term support for these rotational closures may in part be bolstered by people's cognitive biases regarding how they remember experiences [i.e., peak-end heuristic (28)]; there may be opportunities to better leverage these, and other cognitive biases in marine conservation (27, 54); and 4) there were high levels of participatory decision making among community members and strong social cohesion (whereby leaders played a critical role in knowledge exchange). These are key elements of procedural justice that should form a crucial foundation of marine conservation efforts. Although fish biomass in this bright spot appears to be declining over time, there is hope that this can be reversed by further adapting and refining the management system using both local and scientific knowledge systems to maximize benefits while minimizing ecological impacts (47). Critical to this will be moving from adaptive management to adaptive comanagement by strengthening linkages with scientific and management organizations at larger scales (6).

Methods

Study Sites. Our research was conducted in the coastal communities and associated coral reefs of Muluk and Wadau (Karkar Island), Papua New Guinea (Fig. 1). Both communities are small but growing; Muluk's population nearly doubled between 2001 and 2016, from ∼330 people in 50 households to 615 people in 105 households. Likewise, Wadau's population increased from ∼320 people in 50 households in 2001 to 447 people in 72 households in 2012. Both communities are heavily dependent on agriculture as a primary livelihood activity, with fishing often being considered a secondary livelihood activity (13). Fishers reported that an average of 60% of their catch was consumed at home (max, 100; min, 2; SD, 32.3). This was virtually unchanged from 2001, where fishers reported consuming 58% of their catch (max, 100; min, 10; SD, 33.2). Fish catch was primarily sold within the local village. Only 40% of fishers reported selling their catch in the local market (∼15 km away), and only 13% of fishers reported that this local market was the primary destination for their catch. The communities are socially organized around kinship-based clans (3 in Muluk and 6 in Wadau). Although distinct, the 2 adjacent communities share a common language, cultural practices, and form a single unit of local government.

On Karkar Island, and throughout Papua New Guinea, customary rights over land and sea are constitutionally recognized, which provides a legal basis for communities to develop and implement customary management practices like the rotational closure studied here (55). Although there are numerous international conservation nongovernmental organizations working throughout Papua New Guinea, none works directly in our study sites. Likewise, national and provincial fisheries management agencies have a negligible presence.

Ecological Outcome 1: Fish Biomass. We conducted underwater visual censuses (UVCs) on SCUBA to determine reef fish biomass and benthic cover at 4 to 7 replicate reef sites (Fig. 1 and *SI Appendix*, Table S10). At each site, we surveyed multiple belt transects, totaling 304 belt transects (2001: 40, 50 × 5 m; 2009: 24, 50 × 5 m; 2012: 72, 30 × 5 m; 2016 and 2017: each 84, 30 × 5 m). We estimated the abundance and body size (total length) of all diurnal noncryptic reef fishes via standard belt transects on the reef crest (∼3 m) and reef slope (∼7 m). Species density estimates were converted to biomass (kilograms per hectare per transect) using published species length–weight relationships (56). For 2001, only summary biomass estimates (kilograms per hectare) for 6 key families (Acanthridae, Scaridae, Siganidae, Lutjanidae, Haemulidae, Serranidae) were available. Consequently, temporal comparisons including 2001 are restricted to these families. For all other years (2009 to 2017), we calculated biomass estimates for the entire assemblage, and for 9 key functional fish feeding groups (scrapers/excavators, grazers, browsers, macroinvertivores, microinvertivores, piscivore–invertivores, piscivores, planktivores, and detritivores). In 2016, we complemented this with a series of 10-min timed-swim surveys (4 transects per depth per site, 14-m width; ref. 57) to estimate the biomass of large roving fishes unlikely to be encountered on standard belt transects (specifically mobile piscivores and browsers). We determined the benthic community composition using a point intercept method on the same belt transects as within the UVC surveys, and quantified percent cover of live hard coral (including growth forms), macroalgae (>10-mm height), EAM (algae ≤ 10-mm height), and other living organisms ("others") every 0.5 m (2009, 2012, and 2016) or 1 m (2017) across all transects.

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Live corals were identified to genus level, while reef structural complexity was visually estimated 5 times per transect using a 6-point scale (58) from 2009 to 2017. Unfortunately, benthic surveys in 2001 were not included in the final analysis because of incompatible methodological differences (13).

We used a series of hierarchical models to examine the relationship between log (natural) biomass of fish communities and closure, while accounting for potential effects of structural complexity, depth, and percent cover of hard coral, macroalgae, and EAM (*SI Appendix*, Table S10). The models were developed using the *lmer* function in the *lme4* package in R (59) with site and year included as random effects. We used the *step* function in R to develop the most parsimonious model, then compared Akaike information criterion values of each model with those from a null model (i.e., only the random structure). Given the timed-swim surveys (used for piscivores and browsers) did not correspond to any of the benthic transects, we only included closure in these models. Similarly, the 2001 biomass data did not have complementary benthic data. Thus, we ran a supplemental analysis that examined whether biomass from all years (2001, 2009, 2012, 2016, and 2017) was higher inside closures compared to outside, and then compared this to a null model.

Ecological Outcome 2: Fish Behavior. To explore the efficacy of the closure on reducing fish wariness, we examined how close a diver could approach 6 species of fishes before they fled (FID) in open and closed reefs over time. We build on previous work that compared FID inside and outside a closure at this location (25) by conducting a temporal analysis of how FID changes as reefs are opened and closed. Specifically, we compared FID in Muluk and Wadau in 2009 (Muluk's reefs closed, Wadau's reefs open; Table 1) and 2012 (Muluk's reefs open, Wadau's reefs closed; Table 1) to see how FID changed on the same reefs when open reefs became closed to fishing and when closed reefs became open to fishing. To determine the role of a temporal switch in management impacting the behavior of fishes, we examined and compared FID for 6 commonly targeted reef fish species (orange-lined triggerfish [*Balistapus undulatus*], striated surgeonfish [*Ctenochaetus striatus*], daisy parrotfish [*Chlorurus sordidus*], Bleeker's parrotfish [*Chlorurus bleekeri*], yellowbarred parrotfish [*Scarus dimidiatus*], and dusky parrotfish [*Scarus niger*]) across 2009 and 2012 in both Muluk and Wadau reef areas. Observers swam haphazardly (using SCUBA) throughout the shallow fringing reef (3 to 4 m deep) within reefs that were both open and closed to fishing. Focal fishes were identified and then approached horizontally from a distance of 10 to 15 m; benthic features where the fish was positioned before approaching were noted. When the individual changed behavior (i.e., started to flee), the observer immediately dropped a weighted marker. A second marker was then placed at the benthic feature where the fish had been prior to flight initiation. The distance between the 2 benthic markers was then measured (in centimeters). If the fish exhibited a change in behavior that was not obviously a result of the approaching diver (e.g., it was disturbed by another fish), the trial was abandoned. Care was given to avoid sampling the same fish repeatedly: divers swam 5 to 10 m in the opposite direction before beginning the next trial and continually moved throughout the reef area. To examine the relationship between FID, status (closed, open), and site (Muluk, Wadau), we developed a linear mixed-effect model using the *lmer* function in the R package *lme*, with species included as a random effect.

Users' Perceptions of Livelihood Impacts and Key Traits. In 2017, we conducted a series of qualitative interviews with key informants (clan leaders, community leaders, and knowledgeable fishers). We then content organized these interviews and identified 3 key traits, which we explored using both qualitative and quantitative data collected between 2001 and 2017. Specifically, we collected a total of 184 household surveys to identify the following: 1) users' perceptions of whether and how customary management practices impacted people's livelihoods (i.e., a social outcome); 2) information exchange networks; 3) levels of participation in decision making among community members; and 4) perceived levels of compliance.

Qualitative Interviews. We took an exploratory approach to the qualitative interviews. J.E.C. and J.D.L. sampled 21 clan chiefs, knowledgeable fishers, and community leaders (including elders, a religious leader, and the community chairman) as key informants. In some cases, these were separate categories (i.e., some clan chiefs did not fish, not all elders were clan chiefs), but in many cases, there was overlap between categories (i.e., most clan chiefs fished, all clan chiefs were also considered elders in the community). We selected fishers and elder key informants who were known to be knowledgeable about customary practices. We selected clan chiefs and other key community leaders (religious leader and the community chairman) because of the prominent role they play in the community. In Muluk and Wadau, clan leaders have in-depth knowledge of, and responsibility for, customary management in their clan's reef area, and liaise with their clan's members to make decisions about the reef and coordinate customary traditions. All key informants for this specific study were male, but our complementary research has explored gendered perceptions about ecosystem services (e.g., ref. 60). We conducted key informant interviews (ranging from 10 min to 1 h) in Papua New Guinean Tok Pisin. Questions were broad and open-ended and encompassed the types of customary practices that exist in Muluk and Wadau, whether and how people benefit from these practices, perceptions of what things make Wadau and Muluk's unique compared to those of other communities and places, perceptions of how the customary closure system had been successfully maintained over time, and how transgressions with closure rules are dealt with. Interviews were recorded and translated and transcribed into English by J.B. and J.D.L. J.B. did the initial translation, and interviews were then retranslated by J.D.L., and the 2 versions were compared for consistency.

We then content organized these interviews using thematic, concept-driven coding (61) with themes derived from an initial reading of the interviews. The key themes that emerged included not only the ways that people benefit from the customary practices, but also 3 key traits (*SI Appendix*, Table S1): 1) compliance; 2) participatory decision-making among community members; and 3) leadership and social cohesion. These formed the basis for further exploration using our long-term quantitative socioeconomic data (see below). We triangulated the broad themes that arose in interviews with field notes, observations, and informal interviews made by J.D.L. in 2016, and 2017 (over 7 wk) including the opening of the reef, and extended experience (15 y) in both field sites by J.E.C. For all interviews, informed consent was obtained. This study was approved by the James Cook University human ethics committee.

Quantitative Household Surveys. We systematically surveyed a total of 184 households within each community. Here, we report the results from fishing households surveyed in 2001 ($n = 40$), 2009 ($n = 19$), 2012 ($n = 43$), and 2016 ($n = 82$; a more comprehensive sample was needed for the social network component conducted in 2016). Based on themes arising from our qualitative surveys, we drew upon quantitative household surveys to examine:

1) Perceived benefits of customary management to people's livelihoods. We used a 5-point Likert scale to examine people's perceptions of how management has impacted their livelihoods (ranging from strongly detrimental to strongly beneficial). We used Fisher's exact test to examine whether perceptions that the closure system was detrimental to respondents' livelihoods was related to whether the closure was active or not at the time of the survey (i.e., whether the reef in the village being surveyed was open or closed to fishing).
2) To examine key trait 1 identified from the qualitative interviews (compliance), we used a 4-point Likert scale to assess perceived levels of compliance by asking whether people perceived that all fishers, most, a few, or no one fished in the closures (although 2001 only included a 3-point scale for compliance: few, most, or all people comply). To examine compliance further, we also asked respondents whether they had witnessed someone breaking management rules in the previous 12 mo (62).
3) To examine key trait 2 (participatory decision making among community members), we used a 3-point Likert scale to assess the degree to which people were actively, passively, or not involved in resource management decisions.
4) To explore key trait 3 (leadership and social cohesion), we developed a social network of fisheries-related knowledge exchange (2016 only). Specifically, we asked respondents to nominate people to whom they go for important information and advice (hereafter "knowledge") about fishing and fisheries management. Based on our qualitative interviews, we wanted to explore 3 themes with the social network: the role of leaders in knowledge exchange, the degree of cohesion in the knowledge exchange network, and cross-generational knowledge exchange. We used 2 approaches to analyze these social networks. First, we used an ERGM on directed (i.e., knowledge-seeking) network ties to examine the role of leadership and other social attributes (such as clan membership) in driving the formation and maintenance of knowledge exchange relationships and the level of cohesion in the network (63). ERGMs are statistical models of networks that model each tie as a random variable and specify the probability of observing the network as a function of various local social processes (63). To examine cross-generational information exchange linkages, we divided respondents into 3 cohorts: the youngest quartile (youth), the oldest quartile (elders), and the middle 2 quartiles (middle age). We then used the E–I index to examine the proportion of knowledge exchange ties within (internal) each cohort compared to between (external) cohorts. The E–I index is

calculated as follows: (between cohort ties − within cohort ties)/total ties. A higher E–I index indicates substantial information exchange between cohorts.

Data and Materials Availability. Fish abundance and behavior, benthic cover data, and perceived impacts of closure data are openly available on James Cook University's Tropical Research Hub (https://research.jcu.edu.au/researchdata/default/detail/52061788ee1b2f094195e18ca91d2634/). Raw, anonymized social network data are available upon request from M.L.B. (michele.barnes@jcu.edu.au) with reasonable restrictions that do not compromise research participant privacy and consent, consistent with our human ethics board approval.

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