

RESEARCH ARTICLE

Leveraging sex change in parrotfish to manage fished populations

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Healthy parrotfish (family Scaridae) communities fulfill the essential ecosystem process of herbivory in coral reefs, but artisanal fisheries that target parrotfish have degraded their populations. Outright bans and gear restrictions that do not allow parrotfish capture can effectively protect and restore parrotfish populations. As these management actions would be unfeasible in many places, options that allow some fishing but still encourage population rebuilding need to be considered. The life history of parrotfish complicates management decisions because they transition from a mostly female "initial phase" to an all-male "terminal phase." Size-selective fishing on the largest fish can lead to unnaturally low proportions of males in a population, potentially leading to losses in reproduction. At the same time, these visually distinct life phases could present an opportunity to employ a type of catch restriction that would be easy to understand and monitor. We built an agent-based model of the stoplight parrotfish, Sparisoma viride, which included three possible mechanisms of life-phase transitioning, to predict how this species and others like it might react to catch restrictions based on life phase. We found that restricting catch to only terminal-phase (male) fish typically led to populations of greater abundance and biomass and less-disturbed life-phase ratio, compared to a similar fishing mortality applied to the whole population. This model result highlights a potentially important lesson for all exploited protogynous hermaphrodites: a robust population of initial-phase fish may be key to maximizing reproductive potential when the size at life-phase transition compensates for changes in population structure.

Keywords: Coral reef fisheries; Parrotfish; Fisheries management; Sex change; Protogynous hermaphrodites

Introduction

In coral reef ecosystems, herbivores play a critical role in ecological functioning and often support artisanal fisheries. Herbivorous fish and invertebrates consume macroalgae that would otherwise outcompete slow-growing hard corals for space (Hughes, 1994; Mumby et al., 2006). Parrotfish (family Scaridae), an important family of herbivorous fish, also provide food and income to many fishers and their communities (Dalzell, 1996; Sabetian, 2010; Adam et al., 2015). These small-scale reef fisheries have diminished the abundance, biomass, and average size of herbivores on coral reefs around the world (Hawkins and Roberts, 2003; Bellwood et al., 2004; Newton et al., 2007; McClanahan, 2011; Vallès and Oxenford, 2014). Previous research on parrotfish has focused on understanding their life history and ecological function (Bruggemann, et al.,

Corresponding author: Tyler Pavlowich (tyler.pavlowich@dartmouth.edu) 1994a; 1994b; 1994c; van Rooij et al., 1995; 1996b; Fox and Bellwood, 2007; Burkepile and Hay, 2011), establishing the relationship between parrotfish populations and reef health (Mumby et al., 2006; Kellner et al., 2010), and demonstrating the impacts of fishing on parrotfish (Koslow et al., 1988; Jennings and Lock, 1996; Hawkins and Roberts, 2003).

The connection between fishing pressure, parrotfish populations, and ecological health provides a tangible opportunity to improve the condition of currently overfished coral reefs. Researchers have proposed and garnered support for prohibiting parrotfish capture (Bellwood et al., 2004; Mumby and Steneck, 2008; Hughes et al., 2010), but few intermediate options have been proposed. A ban on parrotfish harvest would undoubtedly achieve ecological outcomes but would likely face harsh social resistance or unacceptably reduce fishers' ability to make a living in some cases, as reported in news stories and personal observations of the lead author (Thompson 2014; Anonymous 2017; T. Pavlowich, personal observation). A better way forward may be with a more nuanced management strategy for parrotfish, or at least a more gradual, less socially disruptive transition from an open access to closed fishery (Bozec et al., 2016). A necessary first step

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is to model parrotfish populations undergoing fishing in order to determine the most important aspects of fishing to control and how populations behave when exploited.

Parrotfish have a complex life history in which individuals can change sex; this complexity must be taken into account when attempting to predict management outcomes. All Caribbean parrotfish are protogynous hermaphrodites, where juvenile fish typically first mature into a mostly-female "initial" life phase, though some species have some individuals that mature directly to males (Robertson and Warner, 1978a). Some female initial-phase fish eventually transition to males but retain the initial-phase coloration, while others transition into a fully-male "terminal" life phase. Terminal-phase males might come to defend a territory and group of breeding females (van Rooij et al., 1996b). Researchers have shown that social conditions, e.g. the presence of a dominant male or the maximum size of fish, usually control the size or age at which fish transition from initial to terminal phase (Robertson and Warner, 1978a; Munday, et al., 2006a; Molloy et al., 2011). Many fish species around the world are protogynous, including economically important species (Alonzo et al., 2008), and fishery scientists have called for explicit incorporation of variability in sexchange dynamics in stock assessments (Armsworth, 2001; Alonzo and Mangel, 2004a; Heppell et al., 2006; Hamilton et al., 2007; Provost and Jensen, 2015). Population models where the size at sex change is assumed constant would not appropriately represent the dynamics of a species where sex change is dependent on social conditions that likely vary over time and fishing scenarios. One challenge of managing protogynous hermaphrodites is that fishing often selects for the largest individuals in the stock, which are typically disproportionately male. This practice leads to concerns that, unlike non-sex-changing species, sperm can become the limiting factor to reproductive output if

males become sufficiently rare in the population (Alonzo and Mangel, 2004a). Empirical studies have shown lifephase ratios skewed towards the female-dominated initial phase in parrotfish (Hawkins and Roberts, 2003; Molloy et al., 2011; O'Farrell et al. 2015a) as well as in other species that undergo size-selective fishing (Heppell et al., 2006; Hamilton et al., 2007).

But what if fishing actually selected fish based on life phase, not size? The initial phase (mostly female) and terminal phase (all male) in parrotfish can easily be distinguished visually (Robertson and Warner, 1978a), as shown in Figure 1. Fishers could harvest fish based on life phase, if the fishing gear allowed them to choose which individual fish are caught or kept. Spearfishing allows fishers to see and choose the fish they target before attempting the catch, and fish traps may allow fishers to return undesirable or illegal individual fish if the traps are checked frequently. Fishing with nets does not afford the option of returning fish to the water alive or in sufficient condition to survive. A harvest control rule based on only catching terminal-phase fish would be easy to understand and monitor and it could limit total fishing mortality by setting aside the initial-phase portion of the population. Of course, unequal fishing pressure could also lead to the sex ratio being skewed in favor of the non-targeted sex. However, parrotfish might be able to compensate by changing the rate or timing of sex change, depending on the cues that trigger life-phase transition and how fast that transition takes place (Alonzo and Mangel, 2004b). Pursuing life-phase-selective regulation of fishing on parrotfish requires first understanding how fishing removal of one life phase might interact with the other population dynamic variables that affect sustainability of the stock.

In this study, we explored the effects of fishing both life phases or only terminal phase on population size, the ratio of initial to terminal phase ("life-phase ratio," a proxy



Figure 1: Visual distinction between terminal-phase and initial-phase fish. Initial phase (IP, mostly females) and terminal phase (TP, all males) of stoplight parrotfish (*Sparisoma viride*) and queen parrotfish (*Scarus vetula*) can be distinguished easily underwater. DOI: https://doi.org/10.1525/elementa.318.f1

for sex ratio), biomass of initial-phase spawning stock (a proxy for female biomass), and catch. Two processes combine to determine population dynamic effects of lifephase-selective fishing. First, putting pressure on only the terminal phase should allow the initial-phase segment of the population to accumulate more individuals and reach larger potential sizes than they would under non-selective fishing. Second, the size or timing at which fish change sex might shift if fishing altered the size structure of the population, depending on the cues and mechanisms governing sex change (Hawkins and Roberts, 2003; Molloy et al., 2011). These two processes lead to competing predictions for the outcomes of terminal-phase-only selection. Catching only terminal-phase fish should increase female biomass because the initial phase faces no fishing mortality. However, harvesting terminal-phase fish, the larger individuals in the population, may also decrease the size at sex change, making the initial phase change sex at a younger age and smaller size, thereby reducing female biomass. But, the extent to which the potential plasticity of sex change will compensate for disproportionate extraction of the terminal-life phase is unclear. Considering fishery yield, restricting catch on part of the population may increase or decrease long-term catch, depending on how the population size and structure responds to life-phase selective fishing pressure.

We developed an agent-based model to address whether or not life phase restrictions could be a means of managing Caribbean parrotfish populations and how the uncertainty of the mechanisms of sex change might affect the outcomes we would predict for a life-phase restriction. We modeled the population dynamics of a single parrotfish species with high ecological and fishery value in the Caribbean: stoplight parrotfish, Sparisoma viride. In addition to its importance, this fish is well studied (Cardwell and Liley, 1991; Koltes, 1993; J Bruggemann et al., 1994; van Rooij et al., 1995; 1996b; van Rooij and Videler, 1997; Choat et al., 2003; Paddack et al., 2009) which made it possible to model effectively. Our model extends the model of stoplight parrotfish created by Bozec et al. (2016) by incorporating life phase and sex change explicitly. And although our model was constructed in an agent-based platform and the model of Bozec et al. (2016) was based on systems dynamics, our model borrowed several key equations and parameter values for the life-history processes represented in their model. We used our model to explore the effects of life-phase selection and size selection separately, as well as the idea of a terminal-phaseonly catch restriction.

This study brings together and advances prior work on managing fishing on hermaphroditic species and on seeking ways to sustain and rebuild depleted parrotfish populations. Bannerot (1984) constructed a model to test the reproductive performance of protogynous compared to gonochoristic (non-sex changing) life histories, then tested it against empirical data from grouper fisheries in Bermuda (Bannerot et al., 1987). They found that protogynous hermaphrodites ought to fare better against fishing, providing that males do not become rare enough to limit successful reproduction. Huntsman and Schaff (1994) used a population model of graysby grouper, Cephalopholis cruentata, to explore the effect of fishing on reproductive success under different scenarios of sex-change plasticity and compensation. They found that these protogynous hermaphrodites were generally more vulnerable to fishing due to effects of sperm limitation, but that this vulnerability may not be the case if fish can adjust the timing of sex change. Alonzo and Mangel (2004a; 2004b) created an individual-based model to assess the dynamics of fishing on hermaphrodites, and parameterized it for California sheepshead, Semicossyphus pulcher. They also found that hermaphrodites could experience sperm limitation, but that the effect again depended on the rule governing sexual transition. Heppell et al. (2006) compared simulated management strategies for gag grouper, Mycteroperca micolepis, with an age-structured model. These researchers found that both reduced female biomass and lack of males (i.e., skewed sex ratio) can inhibit population recovery, and that both should be considered when managing hermaphroditic populations. Bozec et al. (2016) modeled Caribbean parrotfish populations to understand the level of fishing and size selectivity that parrotfish can withstand while continuing to provide enough herbivory to keep coral reef ecosystems functioning. Here, we present and explore the idea of using intentional life-phase selection as a tool for limiting capture of parrotfish and improving population biomass.

Methods

We developed an agent-based population model (ABM) for stoplight parrotfish, *Sparisoma viride*, based largely on previous ABMs and demographic models used to explore the effects of fishing on hermaphroditic fish populations (Alonzo and Mangel, 2004a; 2004b; Bozec et al., 2014). The model was built in NetLogo, a free software for agent-based modeling (Wilensky, 1999). We parameterized our model for stoplight parrotfish in Bonaire, using data from the long-term studies of van Rooij et al. (1996a; 1996b), graciously provided by Shay O'Farrell with permission from van Rooij. Here we present a description of the modeling methods in the standard ODD format of Overview, Design concepts, and Details, as established by Grimm et al. (2006).

Overview

Purpose

The purpose of the model is to explore and compare the effects of restricting fishing mortality to only terminalphase stoplight parrotfish on population metrics and catch. We focused on long-term outcomes associated with the life-phase restriction compared to harvesting both life phases.

State variables and scales

The model has one hierarchical level: individual fish. Individuals are described by the state variables: identity number, fork length, weight, age, and life phase. Lifephase levels are juvenile, initial phase, transitional phase, and terminal phase. We use life phase as a proxy for sex, where initial-phase fish represent females and terminalphase fish represent males. This approach is a simplification of reality; around 10% of initial-phase fish have been observed to be male (Robertson and Warner, 1978a). We consider the implications of this simplifying assumption for the interpretation of model results in the Discussion.

There is no spatial component to the model, other than that it represents one hectare of reef. We tuned the model so that population size and structure when no fishing takes place matches population characteristics observed in the unfished population of one reef in Bonaire (van Rooij et al., 1995), which also occupies approximately one hectare.

The population is characterized by the number of individuals in total, in each life phase, and within different size classes; life-phase ratio (IP:TP); biomass of all fish; and biomass of fish in each life phase. Catch is described by the number of fish caught at each time step, and the weight of fish caught.

Process overview and scheduling

The model operates in weekly time steps. Within each time step, five modules are processed in the following order: growth, life phase transition, maturation, mortality, and recruitment. All individuals, in a random order, process through a module, and then move on to the next module. The order of operations matters for some of the processes and not for others. Life-phase transitions and maturation must occur after growth, because the transitions are based on body size. If growth came after life-phase transition or maturation, some fish would have the incorrect life phase for their body size. Mortality and recruitment could occur either before or after growth and life-phase transition and produce the same results.

Design concepts

Emergence

Population dynamics – changes in population size and length and life-phase distributions – emerge from the combination of larval recruitment, somatic growth, life-phase transitions, and mortality. Fishing mortality is an especially important factor because it imposes variable mortality rates on individual fish of different sizes and life phases.

Sensing

Fish can sense their own size and life phase, as well as the size of all other mature fish in the population. We do not know the mechanism for this assessment; it could come via visual cues, physical interactions with other fish (e.g., chasing, nipping, etc.), or both (Barlow, 1975; Munday et al., 2006b). The size and life phase of an individual fish relative to the rest of the population influences its life-phase transitions and susceptibility to fishing.

Interactions

Life-phase transitions are based on the size of an individual relative to others in their social group. The precise mechanisms that determine which fish change life phase and when are not known for this species, but are thought to involve size-based social hierarchies established and maintained by interactions among fish. The model includes three distinct sex-change rules, each of which we explore to account for this uncertainty.

Stochasticity

The model represents life-phase transitions, movement, and mortality as probabilities, which are therefore stochastic. The processes of growth and recruitment are fixed and deterministic.

Observation

We observed model outcomes at the population level, which includes the distribution of fish within subpopulation-level groups.

Details

Initialization

We began simulations with a population of ten juveniles as an arbitrary, common starting point. The population comes to the same stabilized size regardless of the initial number of individuals. We set the sex-change rule, fishing mortality, size at selection, and life-phase selection to the levels to be tested. We allowed the model to run for 15 years (780 weeks) to initialize and settle into a steady state. We then observed the population and catch every three months for the following five years (260 weeks, 20 observations) to represent the long-term outcomes of each fishing scenario. Simulations arrived at consistent equilibria across multiple runs (Figure S1); 20 iterations was a sufficient number to represent each fishing scenario.

Input

We simulated fishing scenarios for the parameter ranges shown in **Table 1**. We performed these simulations with each sex-change rule separately.

Submodels

Submodels of life-history processes form the skeleton of this population model. The formulas for these processes were chosen from the best available information. For some, the literature provides a good understanding of the process in general and for stoplight parrotfish specifically; the work of Bozec et al. (2016) was particularly influential and useful. For others, we had to use simple formulations and estimate parameter values. In the parameterization procedure, described after the submodel descriptions, having good information on some processes and population characteristics constrained the possible parameter values that could lead to expected outcomes, enhancing our confidence in the estimates.

Reproduction

The model treats reproduction and larval recruitment as constant, such that it does not have a stock-recruitment function. Stock-recruitment relationships are extremely

Table 1: Fishing parameters and their ranges. DOI:https://doi.org/10.1525/elementa.318.t1

Parameter	Range of values
Fishing mortality (probability of dying in one year)	0.0, 0.1, 0.2 0.9
Size at selection (cm)	15, 18, 21, 24, 27, 30
Life phase(s) available	Any, terminal phase only

difficult to establish for coral reef fish because of the influence of long-distance larval dispersal and density-dependent mortality post-larval settlement (Roberts, 1996). For example, O'Farrell et al. (2015a) found no evidence that recruitment of stoplight parrotfish was related to the condition of the adult population in Bermuda, the most isolated reef system in the Western Atlantic. However, some evidence has emerged showing that recruitment is likely to be controlled at least partly by local reproduction (Schultz and Cowen, 1994; Green et al., 2015). Given the difficulties in determining an evidence-based relationship, constant recruitment is a common simplifying assumption in many coral-reef fish models (Kellner et al., 2010; O'Farrell et al., 2015b). Here, 46 juveniles enter the population at one-cm fork length at every time step.

Somatic growth

Individual growth is a function of age that follows the von Bertalanffy growth equation,

$$L(t) = L_{inf} (1 - \exp([-\frac{K}{52}] * [t - t_0]))$$

where L(t) is fork length at time t, L_{inf} is the maximum size, K is the growth coefficient, t is age in weeks, and t_0 is the theoretic age at which fish length is zero. Growth rate is divided by 52 to convert annual increments to weekly increments. Each fish is assigned an individualized value for maximum fork length by drawing from an empiricallyobserved distribution of L_{inf} values, in order to reflect the variation in growth seen in nature (Choat et al., 2003; O'Farrell et al., 2015a). Growth rate of each fish is then assigned according to the following relationship between L_{inf} and K:

$$K = \exp(10.87 - 1.92 \cdot \ln[L_{inf} \cdot 10])$$

where fork length is converted to millimeters to fit the original format of the equation (O'Farrell et al., 2015b). Figure S2A shows growth rate as the relationship between weekly growth increments (g/week) and fork length (cm).

We used the following length-weight relationship to convert fish length, as fork length in cm, to fish weight, as total live weight in kilograms (Froese and Pauly, 2017):

$$weight = 0.0257 * L^{2.93}$$

Maturation and life-phase transition

Fish enter the model as juveniles, then transition to initial phase, and finally to terminal phase. Maturation into initial phase occurs when fish become larger than 15 cm (van Rooij et al., 1996b).

As the mechanism that triggers sex change in stoplight parrotfish is unknown, we modeled life-phase transitions using three plausible processes. First, the probability that a fish transitions from initial to terminal phase could be fixed based on body size. Here, we modeled this relationship as a logistic function where the probability of transition increases with size. The form of the equation is taken from Alonzo and Mangel (2004a):

$$p_{fixed}(L_i) = \frac{1}{1 + \exp(-q_{fixed}[L - L_{tran}])}$$

where p_{fixed} is the probability of transitioning, and the length of an individual (*L*) in relation to the length at which fish have a 50% chance of transitioning (L_{tran}) determine the probability of transition for an individual fish. The rate at which probabilities increase is represented by q_{fixed} .

Stoplight parrotfish may adjust the timing of life-phase transitions according to the social conditions of the local conspecific population, as does the taxonomically close bluehead wrasse, *Thalassoma bifasciatum* (Munday et al., 2006a). We included a second sex-change rule in which the probability of an initial-phase fish transitioning to terminal phase is based on the proportion of adult fish in the population smaller than the initial-phase fish in question. The probability of life-phase transition at a given length is calculated according to the following equation first proposed by Alonzo and Mangel (2004b):

$$p_{rel.freq}(L) = \frac{1}{1 + \exp(-q_{rel.freq}[freq.smaller - freq.smaller_{trans}])}$$

where $p_{rel,freq}$ is the probability of transitioning, the length of an individual (*L*) determines the proportion of smaller fish in the population (*freq.smaller*), and there is some proportion of smaller fish at which fish have a 50% chance of transitioning (*freq.smaller*_{trans}). Therefore, the probability of transitioning at a given length changes as the number of fish larger and smaller than that length change. Again, $q_{rel,freq}$ is the rate at which the probability of transition increases. Figure S2C shows the probability of transitioning from initial phase to terminal phase as a function of fork length (cm) for three scenarios: the fixed size at transition rule, the relative frequency rule under heavy fishing, and the relative frequency rule without fishing.

We also modeled life-phase transitions following the account by van Rooij et al. (1996b) of the territorial system of the stoplight parrotfish population in an approximately one hectare reef in Bonaire. van Rooij and colleagues described a system in which there were 17 territories, each of which was occupied by a single terminal-phase fish and multiple initial-phase fish. There was also a non-territorial "group" area in which multiple terminal- and initial-phase fish resided, as well as fish in the process of transitioning from initial to terminal. If a terminal-phase fish went missing from its territory, a terminal-phase male from the group area would move to and occupy the territory and the accompanying harem of initial-phase females. We modeled this system by creating 18 patches within the model environment: 17 territories and one group area. We assigned a target sex ratio (female:male) for each territory to account for variability in the sex ratio observed within each territory. The target sex ratio was randomly drawn from a normal distribution with a mean of four females for every one male (standard deviation = 1), the same as the mean territorial sex ratio observed by van Rooij et al. (1996b). The sex-change procedure attempts to maintain the target sex ratio assigned to each territory (model parameter *target_territories*) and keep the sex ratio below

a certain threshold in the group area (model parameter threshold_groups). Each territory holds one terminalphase and at least the target number of initial-phase fish. If the terminal-phase fish dies, the largest initial phase in the territory initiates sex change by becoming a "transitional" and moving to the group area. At the same time, the largest terminal phase from the group area moves to the territory. If there are too few initial-phase fish in a territory, initial-phase fish from the group area move in, beginning with the largest. Initial-phase fish in the group area also transition to terminal phase if the sex ratio in the group area drops below the group area threshold. The spatial aspects associated with this sex-change rule have no impact on any other aspect of the model. We could not depict this rule as a function of length under any scenario, hence its absence from the component functions indicated in Figure S2.

In all rules, when a fish is selected to transition to terminal phase, it becomes "transitional phase" for four weeks (van Rooij et al., 1996b), and then becomes terminal phase. During this time, the fish does not figure into the sex-ratio calculations.

Natural mortality

Fish in the model experience mortality from natural causes and from fishing. Natural mortality has two components: predation while the fish are small, and senescence when fish become old (O'Farrell et al., 2015b). Bozec et al. (2016) described natural mortality with two, simple two-parameter equations, which we adopted for our model:

$$M_{pred} = a.pred * \exp(b.pred * L)$$
$$M_{sen} = a.sen * \exp(b.sen * L / L_{inf})$$

where *a.pred* scales predation mortality and *b.pred* determines how quickly it decreases with size. For simplicity, we modeled mortality due to senescence as a function of length, assuming that age and length are strongly correlated. The parameters *a.sen* and *b.sen* control how much and how quickly mortality due to senescence is imposed on fish. Both equations return the probability of dying as a function of fork length. Fish are exposed to both sources of natural mortality at each time step. However, mortality from predation becomes very small by seven-cm fork length, and the probability of dying due to senescence only exceeds one percent at 34-cm fork length. Figure S2B shows the probability each fish has of dying due to natural mortality as a function of fork length (cm).

Fishing mortality

Fishing mortality, *F*, is the instantaneous fishing mortality rate for fish that are fully susceptible to fishing. This parameter integrates aspects of fishing such as the number of fishers, how much time each commits to fishing, gear efficacy, and the proportion of fish encountered that is pursued. Size and life-phase selectivity then modify fishing pressure to determine the probability of an individual fish dying. In the model, fishing mortality is input as an annual value, and then divided by 52 to convert it to weekly time steps. Size selectivity ranges from nearly zero to one, with one being fully susceptible to fishing and the probability of dying equal to the given level of fishing pressure. The equation is the logistic function:

$$s(L) = 1/(1 + \exp\left(-r\left[L - L_f\right]\right))$$

where L_f is the size at which fish have a 50% chance of being selected and *r* is a rate parameter that controls the steepness of the curve. Figure S2D shows the value of selectivity as a function of fork length (cm), where 0 is no chance of being selected and 1 is fully selected. Life-phase selection can take three values: any life phase (except juveniles), terminal only, or initial only. If the life phase of a fish can be taken by the fishery, its probability of dying at each time step is:

$$p_{M.fishing}(L) = 1 - \exp(-\frac{F}{52} * s[L])$$

When initial phase cannot be taken, the probability of initial-phase fish dying due to fishing is zero. Note that in the results, we plotted model outcomes versus fishing mortality given as the probability of a fully-selected fish dying annually. Doing so kept the internal model equations in a familiar format for fishery models and the presentation of results in a more generic, easily understood format. Instantaneous fishing mortality was converted to annual fishing mortality according to the following equation (Haddon, 2011):

proportional annual mortality = $1 - e^{-F}$

The model randomly selects the order of applying the mortality functions for every fish at every time step, i.e., fishing mortality, then natural mortality, or vice versa. This approach avoids problems associated with assuming that one always precedes the other.

We assumed that fishers did not compensate for reduced availability of certain sizes and life phases either by increasing fishing effort, or by altering their selectivity by size or life phase. The assumption of no change in selectivity holds well for fishing gears such as gill nets where fishers do not choose the individual fish they target and cannot return captured fish to the water alive. This assumption may be violated, to a greater or lesser degree, when fishers do have the ability to target individual fish, or when they can release fish after being caught. When spearfishing, for instance, fishers can choose individual fish to pursue (Pavlowich and Kapuscinski, 2017), but whether or not fishers can compensate for restrictions by changing their selectivity depends on whether or not they are ever forced to choose between restricted and unrestricted types of fish while fishing. We could not model this complex dynamic in this version of the model. Also, we had no information to evaluate whether fishers would alter their fishing effort in response to a change in parrotfish regulations. Therefore, we did not include any mechanism for increasing fishing mortality onto available segments of the population when others became prohibited.

Submodel	Parameter	Range	Increments
Natural mortality	a.pred	2.3 to 2.5	0.1
	b.pred	-1.26 to -1.24	0.01
	a.sen	9×10^{-5} to 11×10^{-5}	1×10^{-5}
	b.sen	4.8 to 5.2	0.2
Sex change: fixed	L _{tran}	35 to 40	1
	$q_{\it fixed}$	0.5 to 1.0	0.1
Sex change: relative frequency	$freq.smaller_{trans}$	0.6 to 1.0	0.1
	<i>q</i> _{rel.freq}	11 to 19	1
Sex change: territorial	$target_{territories}$	3.0 to 5.0	0.25
	$threshold_{group}$	1.5 to 3.0	0.25

Table 2: Parameters and the ranges of values used for calibrating model processes. DOI: https://doi.org/10.1525/elementa.318.t2

Model parameterization: calibrating to an unfished population

To calibrate the parameter values of processes for which empirically-derived values are not available, we used the same calibration procedure and the same empirical dataset as used by Bozec et al. (2016). Therefore, the purpose of this procedure was to adapt parameter values found by the previous authors to the agent-based model formulation we present here. We systematically searched for values that led to model outputs that matched observed population characteristics of the unfished population in Bonaire. The case study of Bonaire provides a detailed, rich description of a stoplight parrotfish population that was largely stable over four years of data collection (1988–1992) (van Rooij et al., 1996a; 1996b; van Rooij and Videler, 1997).

We began by tuning the parameters that affect population size, size structure, and maximum age of fish. We then explored those that control sex ratio and life-phase distribution for each sex-change rule. Parameters that control population size and structure are: 1) the recruitment rate; 2) individual growth rate 3) the exponential rate of decline of the probability of dying due to predation (i.e., size-based mortality) and the vertical scalar of that probability; and 4) the onset and rate of increase of the probability of dying due to senescence (Table 1). Many combinations of these parameters could produce reasonable population sizes because recruitment and mortality have balancing effects. In order to constrain the possibilities, we held recruitment constant at 46 individuals per week (per hectare), the level estimated in the model calibration procedure by Bozec et al. (2016) for the Bonaire dataset. We did not alter individual growth either, because good empirical estimates of this species growth function exist, as described above. Further, we kept the form of the natural mortality functions the same as described by O'Farrell et al. (2015b) and used by Bozec et al. (2016). With the inflow and growth of fish and the shape of the mortality function fixed, we proceeded to explore parameter combinations for the natural mortality functions. We determined reasonable ranges of these parameters based on previously published information and preliminary exploration of our model (**Table 2**). Then, we did a direct search for the best combination of values within the reasonable range. We used the RNetlogo package (Thiele, 2014) for running simulations and R statistical software (R Core Team, 2017) for processing results.

We used a full factorial design to test combinations of natural mortality parameters that control population size and size structure, identified the combination that produced outcomes that most closely matched observed populations, fixed parameter values to those best fitting values, and then tested all parameter combinations that relate to sex ratio (Thiele et al., 2014). **Table 2** shows the range and increments of the parameter values tested. We first calibrated the model to size structure because this step determined the number of fish for which the lifephase ratio parameters were then tuned.

For the fixed and relative frequency sex change rules, we ran simulations with an initial population of ten juveniles. For the territorial sex-change rule, we had to begin simulations with fish populating in the territories and group areas, so we used the approximate population structure observed in Bonaire. Simulations were allowed 15 years (780 weeks) to settle into a steady state, after which population characteristics (e.g., population size, biomass, sex ratio, etc.) were recorded every three months (13 weeks) for five years (104 weeks) of simulation. We used the average value from the five years of observations to represent the outcomes from that simulation. We considered variability over multiple points in time instead of multiple runs, because preliminary analyses showed little variation in equilibrium values attributable to the initial trajectory of a simulation. After running all parameter combinations from the full factorial design, we more closely examined those combinations that produced reasonable outcomes for total population size (defined as a value within the 95% CI from Bonaire: 405-475). Applying this condition reduced the number of potential parameter combinations from 500 to 28. Next, we calculated a measure of fit for the size structure of the simulated population (O'Farrell et al., 2015b) to the observed Bonaire population; we used this metric to choose the best-fitting parameter combination

Submodel	Parameter	Definition	Value	Source
Reproduction	n	number of recruits entering the population per week	46	Bozec et al., 2016
	Size at recruitment	fork length of fish upon creation in the model	1 cm	Choat et al., 2003
Growth	L _{inf}	maximum length	39 cm	Bozec et al., 2016
	K	growth coefficient	function of L _{inf}	O'Farrell et al., 2015b
Maturation	Size at maturity	size at which fish become initial phase	15 cm	van Rooij et al., 1996b
Sex change: fixed	L _{tran}	size at which fish have a 50% chance of changing sex	37 cm	calibration ^a
	$q_{_{\mathit{fixed}}}$	transition rate coefficient	0.7	calibration
Sex change: relative frequency	freq.smaller _{trans}	size quantile at which fish have a 50% chance of changing sex	1.0	calibration
	$q_{{\it rel.freq}}$	transition rate coefficient	11	calibration
Sex change: territorial	target _{territories}	target sex ratio assigned to each territory	X~N(4, 1)	van Rooij et al., 1996b
	$threshold_{group}$	target sex ratio assigned to group area	1.75	calibration
Natural mortality	a.pred	predation scalar	2.4	calibration
	b.pred	predation rate coefficient	-1.26	calibration
	a.sen	senescence scalar	0.00011	calibration
	b.sen	senescence rate coefficient	5.2	calibration

Tuble 3. Definition, value used, and reference for each model parameter. Doi: https://doi.org/10.1525/ciementa.516.t.	fable 3: Definition, value used, ar	nd reference for each model	parameter. DOI: https:	://doi.org/10.1525	/elementa.318.t3
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^a Calibration in all cases involved systematically varying parameter values until model outputs coincided with the observed population characteristics of the unfished populations in Bonaire.

from the remaining 28. **Table 3** shows the estimated values for these natural mortality parameters.

Each sex-change rule has two unique parameters which determine the probability of changing life phase and, therefore, control the life-phase ratio and the size distribution of life phases: L_{tran} and q_{fixed} for the fixed rule, *freq.smaller*_{trans} and $q_{rel,freq}$ for the relative frequency rule, and *target*_{territories} and *threshold*_{group} for the territorial rule. To find a reasonable combination of each pair of parameters, we created a range of values that produced the approximate observed sex ratios for unfished populations. We ran simulations for each sex-change parameter combination using the best parameter combination from the population size and size-structure calibration. The simulations yielded fewer than 15 combinations for each sex-change rule whose equilibrium life-phase ratio was within 0.5 of empirically observed ratios in unfished populations, ~2.25 females:males (van Rooij et al., 1996b; O'Farrell et al., 2015a). We then used a measure of fit for the life-phase distribution of the simulated populations to the observed unfished population to choose the best parameter combinations among the options tested (Table 3).

Throughout model development, we continually verified that model processes functioned in the model in the way that we conceptually intended them to function (Yilmaz, 2006). For processes that were a function of length (i.e., growth, fixed sex change, natural mortality, and fishing mortality), we plotted model equations to ensure their form was as expected. For processes that were a function of social conditions (i.e., both flexible sex change rules), we plotted the probabilities of transitioning at each length given a randomly produced population structure. We also followed individual fish using the NetLogo graphical interface to ensure that individual size and probabilities changed as expected as the simulation progressed. All of these procedures helped to verify that we had implemented the desired model processes without error.

Model performance: consistency with previous models

Model outputs from our agent-based model compared well to the outputs of the previously published population models (**Figure 2**; **Table 4**) that we used to develop our model (Bozec et al., 2016). This consistency is expected because we used the recruitment rate derived by Bozec et al. (2016) from empirical data on juvenile mortality (Vallès et al., 2008) and calibrated our mortality and life-phase transition parameters to match the observations by van Rooij et al., 1995) of stoplight parrotfish population size and structure in Bonaire. These outputs thus confirm proper functioning of our model, though they do not contribute new information nor validate the model. To validate the model in the future, outputs will need to be compared to unrelated datasets from unrelated stoplight parrotfish populations.



Figure 2: Observed and simulated size distributions of stoplight parrotfish. Observed values (top panel) are for unfished populations in Bonaire and show the mean and 95% confidence interval (CI) from observations over 5 years. Simulated distributions (remaining panels) are generated by an agent-based model for simulated unfished populations with different sex-change rules. Values for each sex-change rule are the mean and 95% CI from the final 20 runs. DOI: https://doi.org/10.1525/elementa.318.f2

Table 4: Observed and simulated population characteristics. DOI: https://doi.org/10.1525/elementa.318.t4

Population characteristic	Uı	Unfished simulations		Reference	Source	
	Fixed	Relative frequency	Territorial	populations (error)		
Population size (#/ha)	412	416	406	440 (95% CI: 405–475)	van Rooij et al., 1995	
Maximum age (y)	8.9	9.3	8.8	9 (otolith increments)	Choat et al., 2003	
Juvenile mortality (proportion that died within 3 months)	0.96	0.97	0.96	0.97 (no measure of error reported)	Valles et al., 2008	

Simulating fishing scenarios

After verifying that the model worked as intended and calibrating parameters to produce population characteristics of unfished populations, we applied various scenarios of fishing and observed the outcomes. We define a fishing scenario as the combination of fishing pressure, size selection, and life phase selection. We conducted a full factorial design experiment by crossing all of the following parameter levels: probability of fishing mortality from 0 to 0.9 by increments of 0.1; length at selection from 15 cm to 30 cm by increments of 3 cm; and life phases available for capture being either "any", or "terminal only." We ran 20 simulations for 20 years each, and then averaged the final values of population parameters. The responses of population characteristics explored below are population size, total fish biomass, life-phase ratio, and initial-phase biomass.

We also predicted how catch would change with the different fishing scenarios. The model kept track of the number and biomass of fish that died due to fishing mortality at each time step. Recall that the model is based on a one-hectare reef; therefore, the units of catch are number of fish caught per hectare per week and weight of fish caught, in kilograms, per hectare per week. We analyzed catch outcomes versus fishing mortality by visually describing the patterns in the relationships between these two parameters. To evaluate the effect of fishery size selectivity, we performed t-tests to determine if mean values of catch outcomes were significantly different between the lowest (15 cm) and highest (30 cm) values for size at selection. To explore the impact of life-phase selection, we compared outcomes associated with the terminal-only rule to the outcomes when any life phase was susceptible to fishing.

Sensitivity analysis

Sensitivity analyses are of special importance in our models because of any residual concerns about the robustness of model structure and parameters arising from the issues discussed in the Methods section. Some parameters (e.g. recruitment rate) are notoriously difficult to estimate and may involve very large errors, an order of magnitude or more, and great temporal variability. Further, any density dependence that does affect real parameters will introduce systematic variation in their values. Other than the modeling of sex change, we chose to vary estimated parameters one at a time by +/-10% and evaluate effects on population metrics – population size, life-phase ratio, and intial-phase biomass - following Sundelöf (Sundelöf et al., 2010). We considered that the model was more sensitive to parameters that provoked a greater than 10% change in population outcomes.

Results

Population and catch outcomes Population size

The modeled fish population responded as expected to the manipulations in fishing mortality we tested. Life-phase and size selective fishing mortality partitioned the population into susceptible and non-susceptible individuals. Population size decreased as fishing pressure increased for all combinations of size selection and life-phase selection (**Figure 3**). As size at selection decreased, population size decreased because a higher proportion of the population experienced fishing mortality and because fish became susceptible at a younger age (and smaller size) and, therefore, contributed to the population for less time.

Catching only terminal-phase individuals exposed a smaller portion of the population to fishing than fishing



Figure 3: Population size versus fishing parameters. Simulated population size (N) as a function of three aspects of fishing: fishing mortality as proportion of individuals (x-axis), size at 50% probability of selection (line color intensity), and life-phase selection (columns: any life phase captured or terminal phase only). Rows show simulation results under three different sex-change rules (fixed, relative frequency, territories). Blue lines are LOESS-smoothed, locally weighted estimates of the mean; grey shading is the 95% confidence interval (often too small to be visible). DOI: https://doi.org/10.1525/elementa.318.f3

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any life phase, which led to higher population sizes compared to the same fishing pressure applied to any life phase (Figure 3, right column). Also, the size at selection did not affect population size very much when catching only terminal-phase fish. It had almost no effect for the fixed or relative frequency sex-change rules, and only minor influence in the territorial rule. This general lack of effect is because the entire terminal-phase segment of the population was fully susceptible to fishing across the explored range of sizes at selection explored; i.e., the highest size at selection already exposed most terminal-phase fish. The exception was when the size at selection was 30 cm, in which case a portion of smaller terminal-phase fish were less susceptible to fishing and population size increased slightly. Beyond the point where size at selection was greater than the minimum size of terminal-phase fish, increasing the size at selection decreased fishing mortality and allowed larger populations. This effect was most visible at high fishing pressure.

Life-phase ratio

Model outputs of life-phase ratio for each sex-change rule compared very well to observations from real populations. The predicted unfished life-phase ratios were 2.21, 2.24, and 2.43 IP:TP for the fixed, relative frequency, and territorial transition rules. The average ratio observed in Bermuda was 2.43 IP:TP, with a range from 1.88 to 4.0 at three different sites (O'Farrell et al., 2015a).

Fishing any life phase affected life-phase ratio as expected (**Figure 4**, left column). For all sex-change rules, life-phase ratio became more skewed towards the initial phase (i.e., sex ratio increased) as fishing pressure increased. When the probability of sex change was fixed, the life-phase ratio became extremely skewed towards IP.

When the simulated population had plastic sex-change rules (i.e., 'relative frequency' and 'territories'), life-phase ratio usually increased with fishing pressure and lower sizes at selection, though not as dramatically as with the fixed rule.

The exception to this pattern came under the territorial sex-change rule and small sizes at selection with any life phase available for capture. Here, life-phase ratio initially increased with fishing pressure, but then peaked and began to decline. This decline in life-phase ratio happened because initial-phase fish continued to switch to terminal phase when the population was exceedingly low. In doing so, the population did not have enough juveniles maturing into initial-phase fish to keep up with the outflow of initial-phase fish to the terminal phase. However, we cannot say whether fish would continue to follow the same cues and social structuring if population size declined dramatically; this phenomenon merits further study.

Catching only terminal-phase fish reduced life-phase ratio skew (i.e., female:male ratio closer to 2.25) for all sexchange rules, given equal value of fishing mortality and size at selection (Figure 4, right column). Under the fixed sex-change rule, the life-phase ratio reached as high as 66 initial-phase fish for every terminal phase. When only terminal phase could be caught, the highest skew under the most intense fishing was 11 intial phase to terminal phase. For the plastic sex-change rules, sex ratio was typically slightly lower when only terminal-phase fish were caught compared to when any life phase could be caught, when we had originally expected that concentrating fishing pressure onto terminal-phase fish would reduce their relative abundance in the population. This surprising result came from the accumulation of protected initialphase fish, as their eventual transition into the terminal







Figure 5: Initial-phase biomass versus fishing parameters. Initial-phase biomass as a function of three aspects of fishing: fishing mortality, size at 50% selection (line color intensity), and life-phase selection (any life phase captured or terminal phase only). Rows show simulation results under three different sex-change rules. Blue lines are LOESS-smoothed, locally weighted estimates of the mean; grey shading is the 95% confidence interval (often too small to be visible). DOI: https://doi.org/10.1525/elementa.318.f5

Table 5: Differences in catch between size at selection for 30 cm vs 15 cm.^a DOI: https://doi.org/10.1525/elementa.318.t5

Life phases available	Sex-change rule	∆ catch number (ha⁻¹ week⁻¹)	p-value (catch number)	Δ catch weight (kg ha ⁻¹ week ⁻¹)	p-value (catch weight)
Any	Fixed	-0.85	0.043	0.119	0.207
Any	Relative frequency	-0.13	0.007	0.161	0.246
Any	Territorial	-0.55	0.163	0.145	0.228
TP [♭] only	Fixed	0.10	0.775	0.142	0.589
TP only	Relative frequency	-0.75	0.026	-0.349	0.073
TP only	Territorial	-0.30	0.450	0.093	0.687

^a F = 0.9 for all scenarios.

^b Terminal phase.

phase maintained life-phase ratios closer to unfished levels. In the territorial sex-change rule, life-phase ratio never peaked and fell when only terminal phase were caught, because there were always enough initial-phase fish to occupy the territories and transition to terminal phase.

Initial-phase biomass

Initial-phase biomass behaved very similarly to population size, despite the differences in the simulated dynamics of the life-phase ratio (**Figure 5**). Initial-phase biomass decreased with increasing fishing mortality and decreasing size at selection. When catching only terminal-phase fish under plastic sex-change rules, increasing fishing pressure led to decreases in initial-phase biomass, even though no initial-phase fish were harvested (**Figure 5**, right column). In this case, increasing fishing pressure removed fish from the largest size classes, which drove down the size at sex change and caused initial-phase fish to transition to terminal phase at smaller sizes. The initial-phase portion of the population shrunk, with the largest initial-phase individuals transitioning to terminal phase earlier. This earlier transition did not occur, by definition, under the fixed sexchange rule (**Figure 5**, top right panel). Also under this rule, initial-phase biomass declined approximately linearly, whereas biomass reductions were nonlinear under the plastic sex-change rules.

Catch

Different patterns in catch emerged depending on whether any life phase or only terminal-phase fish could be caught. Increasing fishing mortality increased the number of fish caught for all combinations of sex-change rule, size selection, and life-phase selection (**Figure 6**). When any fish could be caught, increasing the size at selection decreased the number of fish caught for all sex-change rules, though not significantly for the territorial rule (**Table 5**). When only terminal-phase fish could be caught, the size at selection mattered little to the number of fish caught.



Figure 6: Number of fish caught versus fishing parameters. Number of fish caught at each time step as a function of three aspects of fishing: fishing mortality, size at 50% selection (line color intensity), and life-phase selection (any life phase captured or terminal phase only). Rows show simulation results under three different sex-change rules. Blue lines are LOESS-smoothed, locally weighted estimates of the mean; grey shading is the 95% confidence interval. DOI: https://doi.org/10.1525/elementa.318.f6



Figure 7: Weight of fish caught versus fishing parameters. Weight of fish caught at each time step as a function of three aspects of fishing: fishing mortality, size at 50% selection (line color intensity), and life-phase selection (any life phase captured or terminal phase only). Rows show simulation results under three different sex-change rules. Blue lines are LOESS-smoothed, locally weighted estimates of the mean; grey shading is the 95% confidence interval. DOI: https://doi.org/10.1525/elementa.318.f7

Fishing mortality affected catch weight differently when any life phase could be caught versus when only terminalphase fish could be caught. When all phases were susceptible to fishing, the weight of the catch first increased with increasing fishing mortality, and then mostly leveled off (**Figure 7**). When only terminal-phase fish were susceptible to fishing, increasing fishing mortality always increased catch weight. Our estimates of catch compared well to those made by Bozec et al. (2016) under comparable fishing scenarios. Their model incorporates populations of four parrotfish species, whereas we only considered one, and stoplight parrotfish represent a little less than one third of parrotfish biomass in their model. The authors estimated annual yield around 60 kg ha⁻¹ year⁻¹ when a 30-cm minimum size was implemented and fishing mortality was greater



Figure 8: Population outcomes versus model parameters related to sex change. Sensitivity of population size (A), life-phase ratio (B), and initial-phase biomass (C) as a proportion of their unfished values (y axes) to 10% perturbations in model parameters that determine the probability of sex change (x axes). The dashed lines show where ±10% change in the population outcomes would be. DOI: https://doi.org/10.1525/elementa.318.f8

than 0.4. Our model predicted around 0.3 kg ha⁻¹ week⁻¹, or 15.6 kg ha⁻¹ year⁻¹, slightly less than one third of the Bozec et al. (2016) estimate for total parrotfish harvest, when fishing mortality was equivalent and any life phase could be harvested. When only terminal-phase fish could be caught, and fishing mortality was 0.9, our model predicted approximately a doubling in catch weight, i.e., over 30 kg ha⁻¹ week⁻¹ from stoplight parrotfish alone.

Sensitivity analysis

Model parameters that determine recruitment and natural mortality were analyzed thoroughly in Bozec et al. (2016). Here, we analyze the parameters that determine the probability of sex change under different sex-change rules. First, none of them had an appreciable effect on population size (**Figure 8A**). The length at transition, L_{tran} , had the biggest impact on life-phase ratio of all parameters for all rules (**Figure 8B**). The parameters that pertained to flexible sex-change rules, *freq.smaller*, $q_{rel,freq'}$ *target*_{territories'} and *threshold*_{group'}, changed life-phase ratio

moderately. For the fixed and relative frequency rules, the parameters that triggered life-phase transition, L_{tran} for fixed and *freq.smaller* for relative frequency, affected life-phase ratio more than the rate coefficient at which the probability changes over size, i.e., q_{fixed} and $q_{rel.freq}$.

When the territorial system described from Bonaire was used to determine sex change, neither of the parameters (*target*_{territories}, *threshold*_{group}) had a disproportionate effect. Note also that the values tested in this sensitivity analysis for the target life-phase ratio (*target*_{territories}) were three and five, rather than plus and minus 10% of four (value used in regular simulations), because a life-phase sex ratio is only ever in integer increments within groups.

All sex-change variables affected IP biomass (**Figure 8C**) in the same direction as they affected life-phase ratio, as would be expected. Greater IP biomass comes at least partly from greater numbers of IP fish in the population, which typically leads to a higher life-phase ratio, i.e., more IP to TP. This higher ratio might not have been the case if the number of males somehow increased more than the number of females. In fact, some mortality parameters have opposing effects on life-phase ratio and IP biomass (Figure S3). On the other hand, the sex-change parameters only operated on the ratio of IP to TP, and a decrease in the proportion of one automatically leads to an increase in the other.

Discussion

This model is the first stoplight parrotfish model, to our knowledge, that includes and compares fixed and plastic sex-change rules. We found that the biggest differences between different sex-change rules were the sex-ratio outcomes, with more minor differences in initial-phase biomass and catch-weight outcomes. We separated life-phase selection from size selection, which allowed us to explore management strategies based on life-phase restrictions. These two model attributes allowed us to examine the effects of fishing on population characteristics related to reproduction in a way that acknowledges the uncertainty around hermaphroditism in this species. We explored management outcomes over a range of values for three aspects of fishing that can be controlled: life-phase selection, size selection, and fishing pressure. Doing so provided the insights discussed below, building on the work of others regarding stoplight parrotfish fishery dynamics (Bozec et al., 2016).

Harvest control rules for stoplight parrotfish

Catch terminal phase only

Limiting fishing to only terminal-phase individuals protected the initial-phase segment of the population, which may be the key to protecting and improving protogynous hermaphrodite populations that have flexible sex-change rules. Limiting the capture to only terminal-phase males improved population metrics, including increased initial-phase biomass and closer-to-normal life-phase ratio compared to fishing on all life phases, when the size at selection and fishing pressure were held constant. With only terminal-phase fishing, two mechanisms drove positive population outcomes. First, eliminating mortality on a large segment of the population (i.e., initial-phase fish) limited the number of fish caught, which increased total population size and IP biomass. Second, the increased IP population, compared to when both life phases were harvested, provided a larger pool of fish from which terminalphase males developed. This larger pool in turn increased the influx and abundance of terminal-phase fish, even though only terminal-phase fish were being harvested. Fishing mortality drove down the size at sex change when the size at sex change was flexible and only terminalphase fish were harvested, an outcome observed in all fishing scenarios. In the terminal-phase-only fishing scenario, however, the relief from fishing mortality for initialphase fish more than compensated for this early exiting of some fish to the terminal phase. Therefore, fishing only terminal-phase fish left greater numbers and biomass of initial-phase fish and dampened the skew of the lifephase ratio. Note, however, that our model ignored any potential local stock-recruitment relationship and effects of life-phase-ratio skew on reproduction. If new empirical information determines how local adult populations affect recruitment or shows that deviations in life-phase ratio highly impact reproduction, these results should be re-examined.

Limiting harvest to only terminal-phase fish also increased catch weight compared to harvesting any life phase under the same levels of fishing mortality and size selection. This increase in the biomass of captured fish came while landing fewer fish, meaning that fish were on average substantially larger in the terminal-only scenario. This increase in size would translate into increased income for fishers, assuming fish are bought and sold by weight. Therefore, this regulation presents a win-win for improving ecological and economic outcomes. Factors such as the catchability of fish at different sizes and the market preference for fish size could influence whether fishers actually receive a financial benefit from catching only terminal-phase fish, but the improved stock status at least presents the opportunity.

Previous studies have suggested keeping the size at selection above the average size at sex change, which is essentially the same as a terminal-only rule, to avoid sperm limitation (Alonzo and Mangel, 2004b). Though we did not consider sperm and eggs in this model, we did find that the ratio of initial- to terminal-phase fish under the terminal-only rule remained closer to typical unfished populations than when any life phase could be caught, invoking less concern over an under-abundance of males. Furthermore, sperm limitation is probably a preferable condition to egg limitation (the normal situation for most animal populations), because protogynous hermaphrodites can produce more males faster than gonochoristic species. However, targeting terminal-phase fish and relying on transition from the stock of initial-phase fish could lead to a population with smaller males. This outcome could potentially disrupt social dynamics within the population or impact fertilization rates, especially if sex change is regulated by terminal-phase fish suppressing the transition of initial-phase challengers (Robertson, 1972). Given the uncertainty of how altered social structures might affect reproduction, Alonzo and Mangel (2004) recommended a precautionary approach of keeping fishing mortality low enough to allow some males of all sizes to escape. Of course, complete absence of males in a population or lowering male abundance below thresholds beyond which males can no longer fertilize females could lead to reproductive failure (Alonzo et al., 2008).

Harvesting only terminal-phase individuals might work for other protogynous hermaphroditic species in addition to stoplight parrotfish, assuming the presence of three requisite characteristics: fishers can easily and reliably distinguish the sex of an individual fish, the fishing gear used can select individual fish or safely release those not meeting selection criteria, and the species must have a plastic size at sex change that responds to social cues when the population needs more males. Parrotfish (*Scaridae*) and closely related wrasses (*Labridae*) usually have distinguishable life phases (Robertson and Warner, 1978a; Robertson and Warner, 1978b), whereas groupers (*Epinephelinae*) and snappers (*Lutjanidae*) typically do not. Spearfishing is the most selective gear type possible, although hook and line and fish pots can also allow nonlethal release of undesired individual fish when used in relatively shallow water. Many fish do show flexibility in size at sex change (Warner, 1988; Munday et al., 2006b; Hamilton et al., 2007; McBride and Richardson, 2007; Molloy et al., 2011; Yamaguchi et al., 2013), but scientists should evaluate evidence for each species before managers attempt to use a life-phase regulation.

Size restrictions

Harvesting only terminal-phase fish had approximately equivalent effects on population size and initial-phase biomass as selecting fish at 27–30 cm regardless of life phase (**Figures 4** and **5**). Regulating capture by terminal-phase selection could be preferable to size regulations in fisheries that use spearfishing because visual differences between life phases may make it easier for fishers to accurately distinguish between legal and illegal fish while fishing, and for managers to monitor the catch. Certainly, spearfishers should be able to visually distinguish between life phases of fish they encounter underwater more readily than to visually estimate whether a fish is larger than a minimum size.

Managers looking to improve the status of a stoplight parrotfish population when an outright ban is not possible could experiment with (Walters and Holling, 1990) and closely monitor (Walters, 2007) a terminal-phase restriction on a small scale. The biggest risk associated with this approach is that populations might not receive the cues to change sex or be able to transition as easily as they could in our model. If parrotfish populations cannot compensate readily, a lack of males could lead to extreme sperm limitation and reproductive failure in the worst-case scenario. Implementing this type of rule in conjunction with a functioning marine reserve may allow a margin of safety if males from the reserve can fill in for males that have been fished out. In any case, visual censuses should be conducted frequently to allow early detection and correction of problems.

General lessons for managing fishing of protogynous hermaphrodites

This modeling exercise suggests several general principles for managing protogynous hermaphrodites. First, a robust population of female fish is key to maximizing reproductive potential when the size at sex change can compensate for changes in population structure (Heppell et al., 2006). A robust female population provides a healthy stock from which male fish develop, in addition to enhancing fecundity. In our model, this phenomenon was reflected in the less-skewed life-phase ratio when initial-phase fish received full protection compared to when both life phases were caught (**Figure 4**).

Second, sex-ratio skew is less problematic than diminishing female biomass when the size at which fish become susceptible to fishing is less than the average size at sex change. When size at selection in our simulations was relatively small and fishing pressure was high, the female segment of the population experienced considerable fishing mortality and declined. This decline, in turn, led to the negative consequences of reduced female biomass and, therefore, reduced population fecundity. Conversely, the male segment of the population increased when the size at selection was higher than the size at sex change. In the absence of life-phase regulations, maintaining the size at selection above the size at sex change should assure that females experience little fishing mortality and that males do not completely disappear (Alonzo and Mangel, 2004b; Heppell et al., 2006).

Third, plastic sex-change rules may decrease, but not eliminate, sex-ratio skew caused by fishing. The plastic sex-change rules that we used made fish change sex at smaller sizes as the size structure of the population shifted towards more small individuals and as males were removed by fishing. This shifting kept the life-phase ratio closer to its unfished value than if the size or age at sex change were fixed (Alonzo and Mangel, 2004b; Alonzo et al., 2008). However, fishing still removed terminal-phase fish faster than the population could replace them, and the relative proportion of males decreased. Perhaps the most unexpected outcome from the modeling was the decline in life-phase ratio at high fishing mortality when using the territorial sex-change rule. If territories are the major factor structuring life-phase transitions and social dynamics in stoplight parrotfish, populations may react much differently to fishing pressure than species that are not territorial and are cued to change sex during spawning aggregations (Alonzo and Mangel, 2004b).

Future work

This study demonstrates the importance of including a realistic sex-change rule into parrotfish population models. Doing so can present opportunities for novel management approaches, like those we explored here, as well as point to potential risks for hermaphroditic species. Future research into the cues and conditions that trigger individuals to change sex (Robertson, 1972; Lutnesky, 1994; Yamaguchi et al., 2013) would lend more confidence to predictions made regarding life-phase selective fishing.

An area of research that would improve our model further would be to study how fishers react to restrictions on certain types of fish. In our model, fishing effort directed towards terminal-phase fish did not increase when fishers were prohibited from catching initial phase, nor did fishers increase the time they spent fishing. Details of the type of fishing that takes place and the effort fishers currently and possibly could exert would determine whether or not this assumption is valid for a particular fishery (Pavlowich and Kapuscinski, 2017). In the case of spearfishing, fishers may be able to shift their efforts to terminal phase because they have complete control over which fish to pursue. However, spearfishers would have to encounter initial- and terminalphase fish at the same time for fishers to be able to shift pressure from one life phase to another rather than simply experiencing a decrease in the number of fish they could pursue. Also, fishers may be able to fish more hours in a day or more days in a week to maintain the same total catch, even with a lower catch rate. The more fishers can compensate by effectively refocusing their targeting decisions or increasing fishing effort, the less effective this regulation would be. Of course, the quality of monitoring and

enforcement will play a large role in determining outcomes and must be considered alongside the biological factors of this or any proposed regulation.

Data Accessibility Statement

The model used to run the simulations included in this article are included in the supplemental information.

Supplemental files

The supplemental files for this article can be found as follows:

- **Figure S1.** Population size tracked for five model runs. DOI: https://doi.org/10.1525/elementa.318.s1
- **Figure S2.** Life history processes shown as a function of fork length. DOI: https://doi.org/10.1525/elementa.318.s1
- **Figure S3.** Population outcomes versus model parameters related to recruitment and mortality. DOI: https://doi.org/10.1525/elementa.318.s1
- **Stoplight parrotfish agent-based model.** The population model of stoplight parrotfish used to test regulations based on life-phase restrictions. DOI: https://doi.org/10.1525/elementa.318.s2

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Competing interests

The authors have no competing interests to declare.

Author contributions

- $\cdot\,$ Contributed to conception and design: TP, DGW, ARK
- Contributed to acquisition of data: TP
- Contributed to analysis and interpretation of data: TP, DGW, ARK
- $\cdot\,$ Drafted and/or revised the article: TP, DGW, ARK
- Approved the submitted version for publication: TP, DGW, ARK

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