

Improving Utilization of the Queen Conch (*Aliger Gigas*) Resource in the Colombian Caribbean

A Bioeconomic Model of Rotational Harvesting

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Abstract

A bioeconomic model was developed to examine optimal exploitation strategies for the queen conch (*Aliger gigas*) resource in the Colombian Caribbean. The analysis revealed that ecological and economic performance is maximized under a rotational harvesting scheme whereby fishing takes place following a four-year closure period. Closures allow queen conch biomass to recover and accumulate undisturbed, leading to a 11% increase in stocks as compared to sustained annual harvest. Closures also resulted in a 26% increase in long-term economic benefits upon reopening of the fishing grounds. Results were found to be robust with respect to a number of model assumptions. Policy implications are discussed.

Keywords: co-management; fisheries management; fishing dynamics; rotational harvest; spatial management

JEL Codes: Q01; Q22; Q56

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1. Introduction

Although queen conch (QC) *Aliger gigas* was historically found in high numbers across the Colombian Caribbean, the fishery has been teetering towards collapse since the mid-2000s (Prada *et al.* 2009; Prada *et al.*, 2017). Their slow growth, late maturation and occurrence in shallow waters make QC particularly vulnerable to overfishing. At present, the Colombian QC resource supports an artisanal, subsistence fishery with conservation of stocks clearly identified as the paramount management goal. Since 2010, the management “status quo” (SQ) of the fishery has been defined by (i) a conservation rule restricting harvesting to 8% of the total exploitable biomass (Medley, 2008; Smikle, 2010) and (ii) gear restrictions. Rethinking this status quo may be policy relevant, because sustained annual harvest of fishing grounds may increase the chance of stock collapse and economic failure (Phillips and Boutillier, 1998). For example, the conservation rule neglects important economic factors such as increases in fishing costs associated with declining stocks and trips to distant fishing grounds. Consequently, fishing incomes have declined substantially in recent years, threatening the economic viability of the fishery. On the other hand, gear restrictions such as banishment of diving gear (i.e., scuba and hookah) fail to consider that fishing in shallow waters is biased towards younger conchs, and that fisherfolk are nevertheless forced to search for older (bigger) conchs in deeper waters without the help of diving gear in order to break even financially.

A bioeconomic model was developed in this study to investigate the potential ecological and economic benefits of rotational-harvest management (RM) and contrast these results against the current management framework based on sustained annual harvests. Rotational management has been proposed as an effective management strategy to promote recovery of sedentary stocks (Hart, 2002; Purcell, 2010) and enhance profitability of associated fisheries (Valderrama and Anderson, 2007). The QC resource is a good candidate for RM because the species exhibits low motility and natural mortality and is relatively long-lived. Rotational management plans have been successfully implemented for a wide variety of sedentary species such as abalone, corals, geoduck clams, sea urchins, scallops and cucumbers (Sluczanowski, 1984; Caddy, 1993; Heizer, 1993; Campbell *et al.*, 1998; Lai and Bradbury, 1998; Myers *et al.*, 2000; Pfister and Bradbury, 1996; Hart, 2002; Valderrama and Anderson, 2007; Plagányi *et al.*, 2015). Following multi-year closure periods that are sufficiently long to recover QC stocks, harvest at exploitation rates higher than those recommended by the conservation rule might be sustainably implemented and could lead to increased incomes for fishery communities. Along with the reintroduction of diving gear,

managing for the optimal timing of closures and reopenings at sustainable exploitation rates may also increase fishing efficiency (Myers *et al.*, 2000; Hebert, 2012).

A transition from the management SQ in favor of RM may impose short-term economic losses that are politically infeasible or socially unacceptable (Christie, 2004; Foale and Manele, 2004). Ensuring long-term economic benefits through science-based assessments and strategic planning are a key component to offset many of the short-term costs and potential conflicts associated with the management reforms needed to improve fishery performance (Costello *et al.*, 2016). Both the SQ and RM are focused on preventing tipping points beyond which fishery collapse may be irreversible (Hilborn and Walters, 1992); however, RM also places emphasis on economic factors that are essential to the rebuilding process. One major driver behind this study was to examine the potential economic gains associated with higher-value markets, i.e., exports to international markets. The bioeconomic model also provides guidance on the management strategies most conducive to the production of high-quality conch products, i.e., pearls, from the QC fishery.

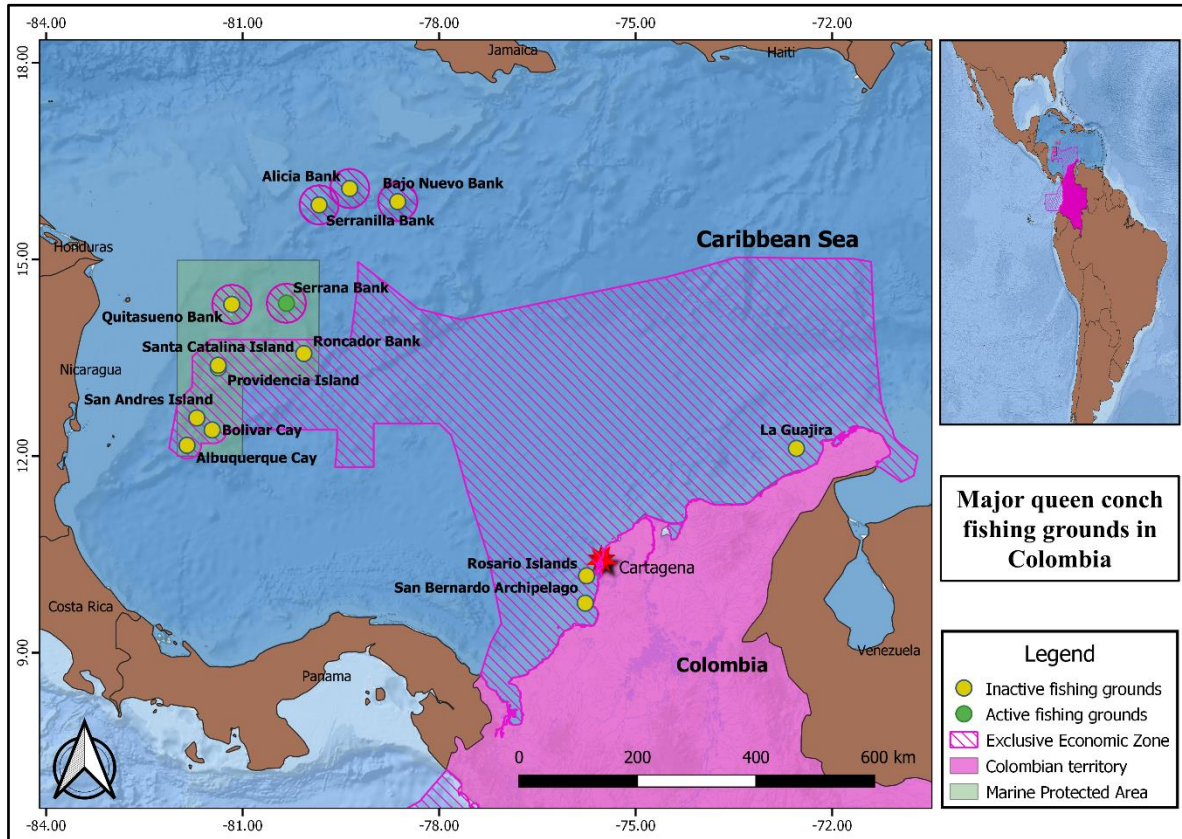
Section 2 in this article provides a brief description of the QC fishery. Section 3 illustrates the potential benefits associated with RM, while Section 4 presents the bioeconomic model. Results are summarized and discussed in Section 5, with conclusions presented in Section 6.

2. The Colombian QC Fishery

2.1 Description of the Fishery

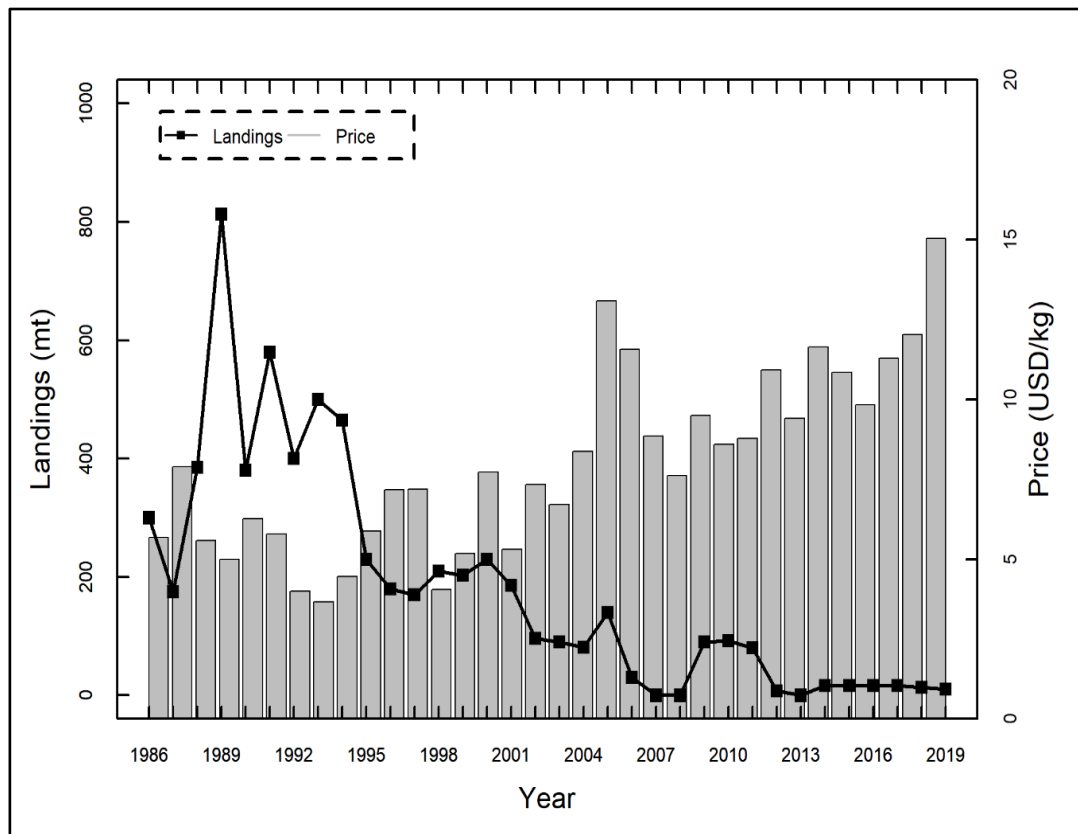
Marine areas with current or historic conch populations in Colombia include the oceanic archipelago of San Andres, Providencia and Santa Catalina (ASPC) in the northern Colombian Caribbean, in addition to the San Bernardo archipelago and Rosario islands, closer to the mainland (Figure 1). In response to growing demand from international markets, an industrial fishery emerged in the mid-1980s and experienced substantial development through the early 1990s. However, different views on fishery management goals, in conjunction with ineffective institutional coordination, triggered competition and conflicts between the artisanal and industrial fleets. Intensive fishing pressure stimulated by the open-access conditions seriously undermined the sustainability of the fishery. In consequence, industrial fishing was banned in 2012, as the remaining stocks were deemed incapable of supporting high levels of fishing activity. At present, fishing is only allowed at Serrana Bank (Figure 1), with all other fishing grounds remaining closed for the foreseeable future.

Figure 1. Major queen conch fishing grounds in Colombia. Map developed by the authors using the software QGIS v3.6.2.



Historical landings peaked in the late 1980s at around 800 metric tons (mt) and declined substantially afterward (Figure 2). Both QC and spiny lobster *Panulirus argus* have traditionally supported the most important capture fisheries in the Colombian Caribbean. In QC fisheries, meat is the major commodity by weight but pearls are more valuable (Appeldoorn, 2013). Shells have also been traded in the international market. During 2000-2003, Colombia QC exports exceeded USD 3.2 million, with pearls, meat and shells accounting for 63%, 36% and 1% of the export value, respectively (Prada *et al.* 2009; CITES, 2019; NMFS, 2020). However, since 2004, the fishery has morphed from a largely export-oriented fishery – the fourth largest in the southwestern Caribbean – to a fishery devoted to domestic markets, yielding very low harvest levels (around 10mt annually; Figure 2).

Figure 2. Historical landings of queen conch in Colombia and price of conch meat in international markets. Prices in the domestic market are around 3-5 USD/kg. Sources: Prada *et al.* (2017), CITES (2019) and NMFS (2020).



In addition to overfishing, illegal pearl trade and illegal, unreported, and unregulated (IUU) fishing are major management challenges in the QC fishery. Because the pearl trade takes place illegally, there is no regulation or clear information on the participating economic agents. As a result, the illegal pearl trade generates high but unequal levels of income, with intermediaries usually extracting the highest benefits. Regarding IUU fishing, the estimated number of IUU fishers in 2004 was approximately 400, which was twice the number of legally registered fishers (Prada *et al.*, 2009). IUU fishing was estimated at 9.8mt in 2019, matching the entire annual quota for the QC fishery (AUNAP¹, personal communication, November 28, 2019).

With around 90 fishers and 15 vessels formally involved, conch fishing remains an artisanal occupation in Colombia (Prada *et al.*, 2017). Nevertheless, it is difficult to identify the level of informal participation in the fishery. The typical fishing unit consists of a 7-to-

¹ Spanish acronym for National Authority for Aquaculture and Fisheries.

10m vessel powered by outboard engines and manned by a captain and three to five crew members. The captain usually receives a higher share of fishing revenues, with the remaining portion divided equally among the crew. Effort tends to be devoted exclusively to queen conch.

Local communities derive benefits from the QC fishery either directly or indirectly, as it contributes to higher incomes, food security and poverty alleviation. The fishery is also a source of social and cultural identity; for example, conch meat is an important component of the local diet and conch fishing is a popular recreational activity.

2.2 The Management System

The current management system is aimed at enhancing stock recruitment through a series of regulations restricting fishing pressure. Its major features are summarized in Table 1.

Table 1. Management system for the Colombian QC fishery, as implemented in 2019.

Management System	Description
Access	Regulated open access. Cooperatives as well participating fishers must hold permits and register boats.
Season length	From November through May – fishing is not allowed during the reproductive season (June 1-October 31).
Exploitable biomass	Control rule based on harvesting 8% of the estimated exploitable biomass (Medley, 2008; Smikle, 2010).
Catch quota	The annual, fishery-wide total allowable catch (TAC) of clean meat is 10 mt. The annual TAC is allocated among fishing cooperatives.
Minimum size	Minimal meat weight for adults is 225g (uncleaned) or 100g (clean). Conchs with a lip size of at least 7mm and shell length exceeding 24cm are considered adults.
Fishing techniques	Manual collection by free diving. Diving gear is prohibited.
Protected areas	Seaflower Marine Protected Area (MPA) established in 2005 (Taylor <i>et al</i> , 2013). Queen conch selected as one of the key bio-indicators to measure the effectiveness of the MPA (Prada <i>et al.</i> , 2009). Seaflower encloses seven of ten major fishing grounds in the ASPC, restricting exploitation.
Exports	International trade regulated by CITES and the FAO Code of Conduct for Responsible Fisheries. No exports are currently allowed.

In addition to national regulations, a ten-year Regional QC Fisheries Management and Conservation Plan was released in 2017 (Prada *et al.*, 2017). The Regional Plan encourages signatory countries across the wider Caribbean to (i) strengthen cooperation and coordination efforts to combat IUU fishing; (ii) gradually introduce co-management schemes; and (iii) improve data collection and traceability of conch products throughout the value chain.

Moreover, Colombia is developing its National Plan, which would introduce management actions complementary to those recommended in the Regional Plan (MinAmbiente, 2018). One of the major recommendations in the National Plan is the implementation of a rights-based management system aimed at restoring the rents historically dissipated by open-access conditions (Clark and Munro, 1980). Although recommendations from both plans have not been implemented yet, it is obvious that the Colombian QC fishery would benefit from properly designed management reforms. Given this context, the bioeconomic model developed in this study aims to explore the potential of rotational harvesting as a key component of the innovative spatial, rights-based management systems currently proposed for the fishery.

2.3 Rationale for Sustained Annual Harvest Management and Gear Restrictions

Conchs rely on mate-pairing and copulation (Davis, 2000) rather than broadcast spawning or other mating strategies that would require fewer reproductive conchs (Spade *et al.*, 2010). Every year during the reproductive months, queen conchs tend to aggregate in the same locations at densities between 100-200 adults/ha (Posada *et al.*, 1997; Appeldoorn *et al.*, 2003; Marshak *et al.*, 2006). The benefits of maintaining reproductive aggregations at their natural densities are twofold (Appeldoorn, 1997; Appeldoorn *et al.*, 2011). First, conch reproduction is negligible at densities below 50 adults/ha due to a pronounced Allee effect² (Stoner and Ray-Culp, 2000). Densities around 100 adults/ha are recommended to ensure successful reproduction within the mating area (Stoner *et al.*, 2011). Second, higher densities of adults seem to enhance the quality of habitat for juveniles (Stoner *et al.*, 1995). For these reasons, conch fishing is only allowed in areas exceeding the threshold density of 50 adults/ha in order to avoid collapse of the stock.

² An Allee effect is a positive association between absolute average individual fitness and population size over some finite interval. Population growth of populations subject to Allee effects is reduced at low density (Drake and Kramer, 2011).

Therefore, gear restrictions have been introduced to (i) limit fishing pressure, (ii) protect conch spawning areas, and (iii) reduce diving-related injuries, given the lack of formal training and the widespread use of obsolete diving technologies among fishers (Tewfik, 2002).

3. Beyond the Status Quo Scenario: Rethinking QC Fishery Management

QC rely on a variety of habitats throughout their life cycle. Planktonic larvae settle to the bottom once a suitable habitat is identified. Immature conchs (< three-years old) are more often found in the shallow waters (5-10m deep) of coastal wetlands and seagrass beds. Mature conchs (> three-years old) inhabit seagrass beds and sand flats in the 4-18m range in the absence of fishing pressure (Weil and Laughlin, 1984). If fishing occurs, adults are more often found in the deeper 10-30m range (Torres-Rosado, 1987; Stoner and Schwarte, 1994).

Because gear restrictions constrain fishing to largely free diving methods, immature conchs are more vulnerable to exploitation than older conchs, as the former tend to inhabit the shallow waters accessible by free diving (Lagos-Bayona, 1994; Hernández-Barrero *et al.*, 1997a). This age bias is detrimental to the fishery because it limits the future reproductive potential of conch populations, given that immature conchs comprise a major portion of harvests. In addition, it impacts profitability because clean meat of immature conchs weighs between 50%-60% less than adults (Hernández-Barrero *et al.*, 1997a), meaning that harvesting two immature conchs generates the same benefits as harvesting one adult. Gear restrictions also increase the risks associated with fishing. To increase catch per unit of effort (CPUE) in depleted areas, fishers must explore deeper locations without the help of diving gear and without a clear understanding of the health effects associated with free diving in deep locations (Tewfik, 2002).

The overall decline in landings and exports has dramatically reduced the number of direct and indirect jobs created by the fishery. Meat prices are lower in the domestic market, leading to further declines in revenues. In addition, the search for large QC aggregations have forced fishers based in the San Andres and Providencia islands to traverse longer distances to reach Serrana Bank (Figure 1), increasing fuel and ice costs. This situation has indirectly contributed to overfishing and the rapid fulfillment of the annual quota as fishers increase their harvests to ensure profitability in each trip.

4. The Bioeconomic Model

The model was designed to compare the ecological and economic performance of two different management strategies – SQ versus RM – in five fishing grounds: Alicia, Serranilla,

Bajo Nuevo, Quitasueño and Serrana Banks (Figure 1), henceforth denoted in the aggregate as the Rotational Area (RA). These five banks were identified as the grounds with the largest potential to support commercial activity (including exports to international markets) in the future (MinAmbiente, 2018). In order to meet the food security requirements of local communities, a separate quota for subsistence fisheries must be allocated to the other fishing areas in the ASPC.

The model contains two decision variables: (i) the allowable harvest rate, and (ii) the frequency of openings. The aim of the model is to determine the exploitation strategy leading to maximization of both ecological and economic performance for a period of 40 years. Ecological and economic performance are evaluated in terms of stock abundance (standing density of conchs) and Net Present Value (NPV) of the fishery, respectively.

The following tradeoff lies at the heart of the model: an increase in the allowable harvest rate enhances economic performance but decreases ecological performance due to declining stock biomass. On the contrary, less frequent openings enhance ecological performance but diminish economic performance. The determination of the optimal exploitation strategy depends on the correct combination of these two choice variables, considering that economic performance is subject to a certain level of ecological performance given the strong Allee effect driving population dynamics. The decision problem facing the resource manager is presented in section 4.5.

The model was designed with simplifying assumptions on aspects such as recruitment, pricing and fishing effort in order to analyze the effects of allowable harvest rate and frequency of openings on both ecological and economic performance. It was also assumed that the pearl trade is regulated in a transparent manner following CITES recommendations (Table 1). Ecological and economic parameters are presented in Tables 2 and 3, respectively.

4.1 Estimation of Total Exploitable Biomass

Conch biometrics is used to estimate the total exploitable biomass at time t , $B^t \in \mathbb{R}_{\geq 0}$, in the Rotational Area. Appeldoorn (1988b) described a model for growth in lip thickness of conchs using the von Bertalanffy growth function:

$$L_a = L_\infty (1 - e^{-\varphi(a-a_0)}) \quad (1)$$

where L_a denotes lip thickness (in cm) at age a (in years), φ is the growth coefficient (in year^{-1}), L_∞ is the maximum lip thickness of conchs (in cm), and a_0 is the age at which the lip would have had zero size. Stoner *et al.* (2012) estimated $L_a \in [13, 19]$ as the size range within which half of the adults are reproducing, which is consistent with reaching sexual maturity at four years of age (Appeldoorn, 2013). According to a number of authors (Márquez-Petrelt, 1993; Márquez and Dávila-Vila, 1994; Márquez-Petrelt *et al.*, 1994), conchs in the Colombian Caribbean have a life expectancy of 12 years, although lifespan has been reported to reach 20–30 years elsewhere in the Caribbean (Appeldoorn, 1994; CFMC, 1999; Ehrhardt and Valle-Esquivel, 2008). The model assumes $a \in [1, A]$, with $A = 25$ (Table 2).

Table 2. Ecological Parameters of the Age-Structured Model for the Colombian Queen Conch Fishery.

Parameter	Description	Value	Source
L_{∞}	Maximum lip thickness of conchs.	35 cm	Gallo-Nieto <i>et al.</i> (1996).
φ	Lip growth coefficient.	0.27/year	Gallo-Nieto <i>et al.</i> (1996).
a_0	Age at which lip thickness is zero.	0	Gallo-Nieto <i>et al.</i> (1996).
A	Longevity of conchs in the Caribbean.	25 years	Appeldoorn (1994), CFMC (1999), Ehrhardt and Valle-Esquivel (2008).
$x; y$	Coefficients in the lip thickness / clean meat weight relationship.	$x = 0.00141; y = 1.5$.	Adapted from Márquez-Pretelt (1993). Consistent with Márquez and Dávila-Vila (1994), Lagos-Bayona (1994), and Hernández-Barrero <i>et al.</i> (1997a, 1997b).
Δt	Time step in simulations.	1 year	
T	Horizon of the model.	40 years	
M_a	Natural mortality rate of conchs at age a ; $a \in [1, A]$.	$M_a = 4.001a^{-0.9226}$ On average, 0.68 year ⁻¹ and around 0.20 year ⁻¹ for older adults	Appeldoorn (1988a). Consistent with Márquez-Petrelt <i>et al.</i> (1994), Gallo-Nieto <i>et al.</i> (1996), Medley (2008).
S	Effective area for conch fishing, which includes five banks: Serranilla, Quitasueño, Serrana, Alicia and Bajo Nuevo (Figure 1).	36,049 hectares.	Prada <i>et al.</i> (2009) and MinAmbiente (2018).
K	Carrying capacity of environment.	350 conchs/ha	Estimated from Márquez-Pretelt (1993), Márquez and Dávila-Vila (1994), Lagos-Bayona (1994), and Hernández-Barrero <i>et al.</i> (1997a, 1997b), Prada <i>et al.</i> (2009) and MinAmbiente (2018).
r	Intrinsic growth rate of conch populations.	0.35	Ibid.

Table 2. Continued.

Parameter	Description	Value	Source
z	Ratio of growth rate r to carrying capacity k .	0.001	Ibid.
q	Catchability coefficient.	1	Prada <i>et al.</i> (2017)
$IUU^t(I)$	Amount of IUU fishing as a function of investment in management, I .	<p>The function is modeled as follows:</p> $\forall I \in \mathbb{R}^+ : IUU(I) = \begin{cases} 0.5B^t & \text{if } 0 < I < \text{USD } 2 \text{ million} \\ 0.25B^t & \text{if } \text{USD } 2 \text{ million} \leq I < \text{USD } 3 \text{ million} \\ 0.05B^t & \text{if } I \geq \text{USD } 3 \text{ million} \end{cases}$ <p>Because investment in management is set between USD 2-2.6 million (Table 3), 25% of the total exploitable biomass is lost through IUU fishing.</p>	(MinAmbiente, 2018; see also Table 3).
μ	Average age of harvested conchs.	5 years in SQ scenario; 7 years in RM scenario.	Value selected by the authors of the model.
σ	Standard deviation of age of harvested conchs.	2 in SQ scenario; 4 in RM scenario.	Ibid.
α	Minimum age of harvested conchs.	3 years in both SQ and RM scenarios.	Ibid.
β	Maximum age of harvested conchs.	7 years in SQ scenario; 25 years in RM scenario.	Ibid.

The relationship between lip thickness and clean meat weight is represented by the following expression

$$W_a = xL_a^y \quad (2)$$

where W_a denotes clean meat (in g) at age a , and x and y are coefficients (Table 2). Clean meat and shells in adult conchs represent around 5 to 10% and 72% of total weight, respectively (Lagos-Bayona, 1994; Hernández-Barrero *et al.*, 1997a).³

The total exploitable biomass B^t (in tons of clean meat) at time t is calculated as

$$B^t = \frac{\sum_{a>2}^A n_a^t W_a}{10^6} \quad (3)$$

where n_a^t denotes the number of conchs of age a at time t . Conchs within $a \leq 2$ are excluded from the estimation of B^t (see equations 1 and 2 and minimum size requirement in Table 1). The model scatters the conch population across age classes $a = \{1, 2, \dots, A\}$ partitioned into discrete time steps $t = \{1, 2, \dots, T\}$, with a time step length $\Delta t = 1$ year and $T = 40$ years (Table 2).

4.2 Natural Population Growth

Age-structured populations at each time step t are tracked by population vectors

$$n^t = \left(n_a^t \right)_{1 \leq a \leq A}. \text{ Total conch population at time } t \text{ is computed by } N^t = \sum_{a=1}^A n_a^t.$$

The main processes affecting natural population growth are natural recruitment at time t , $R^t \in \mathbb{R}_{\geq 0}$ (total number of recruits) and natural mortality at age $a \geq 1$, denoted by $M_a \in \mathbb{R}_{> 0}$ (in year⁻¹). Population dynamics are modeled as follows

$$n^{t+1} = \left(n_1^{t+1} = R^t, n_2^{t+1} = n_1^t e^{-(M_1)\Delta t}, \dots, n_a^{t+1} = n_{a-1}^t e^{-(M_{a-1})\Delta t}, \dots, n_A^{t+1} = n_{A-1}^t e^{-(M_{A-1})\Delta t} \right) \quad (4)$$

where $M_a = 4.001a^{-0.9226}$ (Appeldoorn, 1988a). Note that natural mortality of immature conchs is much higher than that of adult conchs (Appeldoorn, 1988a; Medley, 2008).

³ A number of studies have indicated that female conchs weigh on average 7% more than males of the same age (Randall, 1964; Márquez-Petrelt, 1993; Márquez and Dávila-Vila, 1994; Márquez-Petrelt *et al.*, 1994). For simplicity, this study assumes that conchs of the same age have identical weight, regardless of sex.

Conch fecundity is high (Appeldoorn, 1993) and there is no evidence of senescence with increasing age (Stoner *et al.*, 2011, 2012). Both growth and recruitment rates have been shown to be density dependent. For example, growth declined to zero in an experimental setting when density was increased by a factor of three relative to natural densities. Also, as conch density increases above a certain threshold, recruitment decreases due to lower food availability (Stoner, 1989).

Recruitment at time t is modeled by the Verhulst equation

$$R^t = rd^t - z(d^t)^2 \quad (5)$$

where d^t denotes adult density (adult conchs/ha) at time t . It is computed as $\frac{\sum_{a>z}^A n_a^t}{S}$, with S (in ha) standing for effective area for conch fishing. Further, r is the intrinsic growth rate of the population, and z is the ratio between growth rate and carrying capacity K , $K \in \mathbb{R}_{>0}$. The ratio $z = \frac{r}{K}$ is then a measure of density dependence. Equation 5 can be rewritten as follows

$$R^t = rd^t \left(1 - \frac{d^t}{K}\right) \quad (6)$$

Recruitment tends to zero when d^t tends to K . Natural population growth is represented in a G matrix with $T \times A$ dimensions, where the element G_{ij} of the matrix G represents the number of conchs of age a at time t . For example, $G_{i=20,j=6} = n_{a=6}^{t=20}$, which is the number of conchs aged six years old at the 20th year of the simulation. Note that natural population growth is only constrained by food availability; other environmental conditions remain unaltered.

4.3 Modeling Harvest and Management Scenarios

Total harvest at time t , $h^t \in \mathbb{R}_{\geq 0}$, is modeled according to a modified version of Gordon's traditional model (Gordon, 1954)

$$h^t = q(B^t - IUU^t(I))\eta^t \quad (7)$$

where h^t is a function of (i) the species' catchability coefficient, $q \in [0,1]$ (Table 2); (ii) the allowable harvest rate, $\eta^t \in [0,1]$, defined as a percentage of the total exploitable biomass

B^t ; and (iii) IUU fishing, $IUU^t(I) \in [0, B^t]$, which reduces B^t . As described in section 2.1, substantial IUU fishing takes place in the fishery. Neither SQ nor RM can occur at sustainable levels without investing in monitoring and law enforcement to reduce IUU fishing. Thus, the amount of IUU fishing depends on the investment in management, $I \in \mathbb{R}_{\geq 0}$, and $IUU^t(I)$ is modeled as a step function (Table 2). The level of I is set according to the Colombian National Plan recommendations (Table 3).

Table 3. Economic Parameters of the Age-Structured Model for the Colombian Queen Conch Fishery.

Parameter	Description	Value	Source
m	Historical average price for clean conch meat.	USD 6/kg	Prada <i>et al.</i> (2009); CITES (2019) and NMFS (2020).
\tilde{p}	Price for mid-quality conch pearls in international markets.	USD 1,000/pearl	Prada <i>et al.</i> (2009) and CITES (2019).
\hat{p}	Price for high-quality conch pearls in international markets.	USD 3,000/pearl	Ibid.
τ	Occurrence rate of pearls.	1/1025, i.e., one pearl found in every 1,025 conchs harvested.	Ortegón-Guasca (2006).
$CPUE(d', \bar{W}_{FT})$	Catch per unit of effort as a function of adults density and average weight of harvested conchs	In SQ, $CPUE(d', 0.2) = 0.86d' + 1.81$ (in kg/day/vessel) In RM, $CPUE(d', 0.25) = 1.07d' + 2.26$ (in kg/day/vessel) In both scenarios, 1 vessel = 4 fishers	Estimated from Appeldoorn and Baker (2013) and in-person interviews. ^a
λ_1	Fuel costs per trip.	USD 570/trip	In-person interviews.
λ_2	Ice costs per trip.	USD 372/trip	Ibid.
λ_3	Food and supplies costs per trip.	USD 240/trip	Ibid.
λ_4	Miscellaneous costs per trip.	USD 1,671/trip (SQ scenario); USD 1,915/trip (RM scenario).	Ibid.
\bar{e}	Average number of fishing days per trip.	15 days/trip	Ibid.
κ	Fixed costs.	USD 17,450/year (SQ scenario); USD 22,988/year (RM scenario).	Ibid.
i	Discount rate.	3.73%	DANE (2020).
I	Investment in management programs. ^b	USD 2 million (SQ scenario); USD 2.6 million (RM scenario).	MinAmbiente (2018).

^a In-person interviews with six fishers and two vessel owners were conducted from October 2018 to January 2019 in San Andres and Providencia islands.

^b Investments are made in seven different programs: (1) scientific research; (2) monitoring of harvests; (3) control and surveillance to reduce IUU fishing; (4) education and outreach activities; (5) fishery management; (6) governance and legal framework; and (7) commerce and responsible consumption.

4.3.1 The SQ Scenario

This scenario is a reflection of the current management framework of the fishery. Hence, η^t follows the conservation rule proposed by Medley (2008) and is given by

$$\eta^t : \begin{cases} \text{if } d^t \geq 100 \Rightarrow \eta^t = 0.08 \\ \text{if } 50 \leq d^t < 100 \Rightarrow \eta^t = 0.08 \left(\frac{d^t}{100} \right) \\ \text{if } d^t < 50 \Rightarrow \eta^t = 0 \end{cases} \quad (8)$$

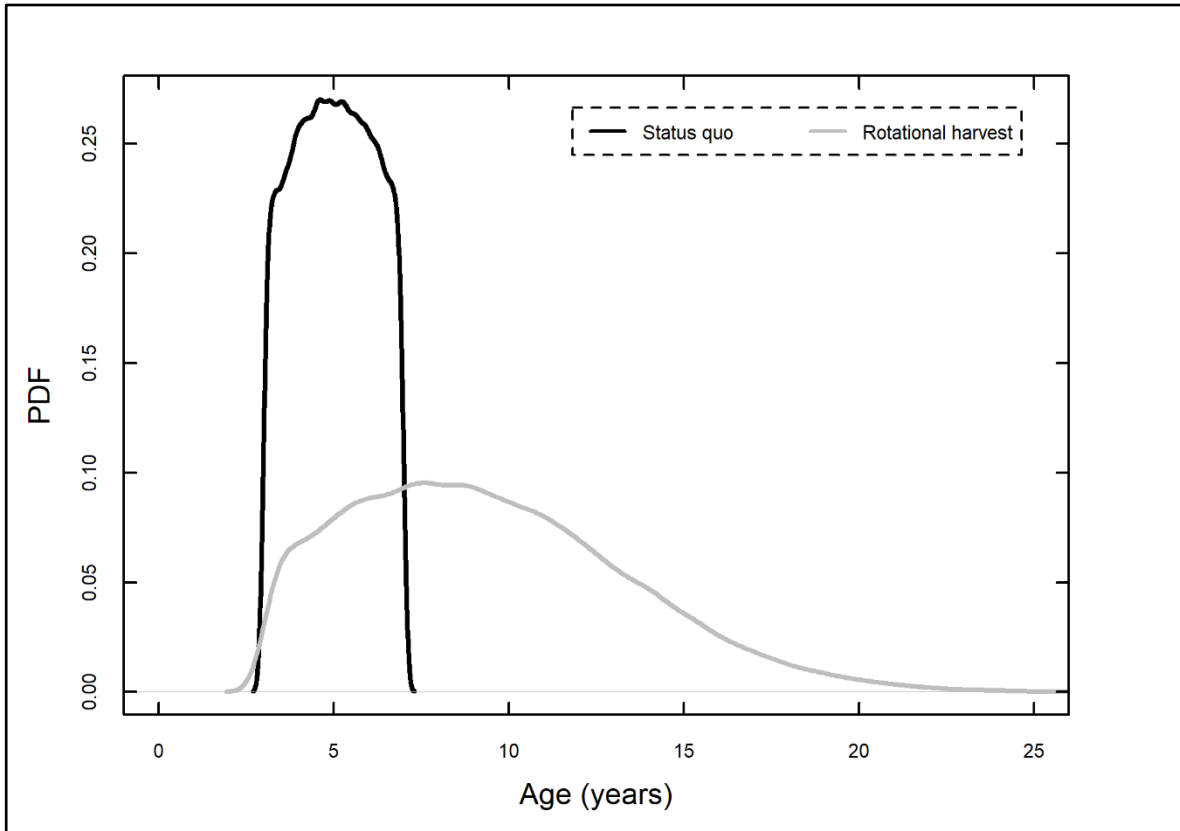
According to equation 8, the allowable harvest rate is maximal ($\eta^t = 0.08$) if adult densities exceed 100 conch/ha, which would ensure the maximum sustainable yield (MSY). Harvest is reduced progressively from 8% to 4% if adult densities fall between 50-100 conch/ha. Harvest is not sustainable if adult densities drop below 50 conch/ha, which corresponds to the minimum stock threshold (MST).

Since diving gear is prohibited in the SQ scenario, younger conchs are more vulnerable to fishing, while older conchs are rarely accessible because they tend to inhabit deeper waters. A truncated normal distribution is employed to simulate how conch fishing is taking place. Let f denote the probability density function (PDF) of age-structured conch populations susceptible to fishing. The function

$$f(a; \mu, \sigma, \alpha, \beta) = \frac{1}{\sigma} \left(\frac{\phi\left(\frac{a-\mu}{\sigma}\right)}{\Phi\left(\frac{\beta-\mu}{\sigma}\right) - \Phi\left(\frac{\alpha-\mu}{\sigma}\right)} \right) \quad (9)$$

allows us to compute the probability that conchs of a certain age a are harvested. Parameter a denotes the age of the conchs, μ is the average age of harvested conchs, σ is the associated standard deviation, and α and β are the lower and upper limits for the function, respectively. The intuition behind this function is that conch harvesting follows the normal distribution, conditioned upon $\alpha < a < \beta$. Thus, ϕ represents the PDF of the standard normal distribution, and Φ is its cumulative distribution function (Table 2). Free diving is characterized by low σ , that is, it targets conchs at specific, young ages (Figure 3).

Figure 3. Probability distribution functions for the SQ and RM scenarios. In the SQ scenario, younger conchs inhabiting shallow waters are more vulnerable to fishing because only free diving is allowed. In the RM scenario, harvested conchs are on average older and bigger as diving gear is reintroduced.



4.3.2 The RM Scenario

Compared to SQ, the allowable harvest rate can be higher in rotational management, $0 \leq \eta^t \leq 0.65$. Diving gear is reintroduced to increase harvest and improve fishing efficiency. Parameters in equation 9 are therefore different from those considered for free diving (Table 2). When diving gears are permitted, a higher σ in equation 9 indicates that conch fishing is much less biased toward younger ages. In both the SQ and RM scenarios, it is assumed that conchs in shallower waters are harvested first because they are the easiest catch. However, RM fishers can also collect conchs in deeper waters. As a result, harvested conchs will be on average older and bigger (Figure 3).

In both SQ and RM scenarios, the number of conchs harvested is represented in an H matrix with $T \times A$ dimensions, where the element H_{ij} of the matrix H represents the number of conchs of age a harvested at time t . The total number of conchs harvested at time t , $\gamma^t \in \mathbb{R}_{\geq 0}$, is given by

$$\gamma^t = \sum_{j=1}^A H_{i=t,j} \quad (10)$$

Once natural population growth and total harvest have been estimated, net population dynamics is represented in a P matrix with $T \times A$ dimensions, where the element $P_{ij} = G_{ij} - H_{ij}$ of the matrix P represents the standing population of age a at time t . The conditions $\forall a < 3, H_{i,j=a} = 0$ and $\forall i \in [t, T], 0 \leq H_{i=t,j} \leq G_{i=t,j}$ always hold. The system will reach a stable equilibrium when $\forall i \in [t, T], P_{i=t,j=1} = \gamma^t$, with $t \leq T$.

4.4 Economics

Economic performance depends on revenues from two conch products: clean meat and pearls. Shells are not introduced in the model due to their low market value. Fishing costs, $c(h^t) \in \mathbb{R}_{\geq 0}$, are proportional to h^t . Net revenue at time t , $\pi^t \in \mathbb{R}_{\geq 0}$, is therefore obtained by subtracting fishing costs from revenues

$$\pi^t = mh^t + p(\gamma^t) - c(h^t) \quad (11)$$

where m and p represent prices (in USD) for clean conch meat and pearls, respectively (Table 3). Hence, mh^t and $p(\gamma^t)$ represent revenues from clean conch meat and pearls, respectively. Revenues from pearls are proportional to the number of harvested conchs γ^t as pearls are detected at a frequency $\tau = \frac{1}{1025}$; i.e., on average, one pearl is found for each 1,025 harvested conchs (Table 3). Conch pearls are extremely rare non-nacreous pearls not currently attainable under farming conditions. Moreover, there is only a one-in-a-ten chance that a pearl will meet high-quality standards in international markets (Ortegón-Guasca, 2006), which makes them incredibly valuable (Anderson, 2015). Revenues from pearls are then estimated as

$$p(\gamma^t) = \gamma^t \tau [0.9\tilde{p} + 0.1\hat{p}] \quad (12)$$

where \tilde{p} and \hat{p} represent mid-quality and high-quality pearl prices in international markets, respectively (Table 3).

Fishing costs include both variable and fixed costs. The function $c(h^t)$ is of the form

$$c(h^t) = \lambda \frac{h^t}{CPUE(d^t, \bar{W}_{FT})} + \kappa \quad (13)$$

where $\frac{h^t}{CPUE(d^t, \bar{W}_{FT})}$ denotes the fishing effort (in fishing days per vessel) at time t , and

$CPUE(d^t, \bar{W}_{FT})$ is CPUE (in kg per day per vessel) as a function of adults density, d^t , and average weight (in kg of clean meat) of conchs harvested employing different fishing techniques (whether free diving, FD, or diving gear, DG), $\bar{W}_{FT \in \{FD, DG\}}$ (Tables 2 and 3). An

increase in adults density and/or average weight increases CPUE, such that $\frac{\partial CPUE}{\partial d'} > 0$ and $\frac{\partial CPUE}{\partial \bar{W}_{FT}} > 0$. Harvested conchs will be on average older and bigger in the RM scenario and therefore $\bar{W}_{DG} > \bar{W}_{FD}$. An important feature of the model is that all vessels have four fishers and are homogeneous with respect to $CPUE(d', \bar{W}_{FT})$. Costs per unit of effort, $\lambda \in \mathbb{R}_{\geq 0}$ (in USD per fishing day per vessel), are calculated as follows

$$\lambda = \frac{\lambda_1 + \lambda_2 + \lambda_3 + \lambda_4}{\bar{e}} \quad (14)$$

where λ_1 , λ_2 , and λ_3 denote the per-trip costs of fuel, ice, and food and supplies, respectively. In turn, λ_4 represents the miscellaneous costs per trip (e.g., the captain's wage, crew costs and costs of renting the vessel) and \bar{e} is the average number of fishing days per trip (Table 3). Thus, the term $\lambda \frac{h'}{CPUE(d', \bar{W}_{FT})} \in \mathbb{R}_{\geq 0}$ encapsulates total variable costs (in USD). Fixed costs $\kappa \in \mathbb{R}_{\geq 0}$ (in USD) include the value of licenses as well as vessel and gear maintenance. To simplify the analysis, the model assumes that the fishing fleet is constant over time (Table 3).

Economic performance is evaluated in terms of NPV over the T period, $NPV_T \in \mathbb{R}$, which is computed as follows:

$$NPV_T = \sum_{t=1}^T \frac{\pi^t}{(1+i)^t} - I \quad (15)$$

On the RHS of equation 15, the numerator and denominator of the first term denote the stream of annual net revenues and the discount rate, respectively (Table 3). In turn, I refers to total investment and includes all activities aimed at combating IUU fishing (equation 7; Table 3).

4.5 The Decision Problem

The decision problem of the resource manager is

$$\underset{\eta^\xi, \xi}{\operatorname{argmax}} \{NPV_T(\eta^\xi, \xi), d(\eta^\xi, \xi)\} \quad (16)$$

where $d = \frac{1}{T} \sum_{t=1}^T d^t$ denotes the average standing density values for conch adults over the T period, under the condition that $\forall t \in [1, T], d^t \geq 50$ holds. The optimal exploitation strategy is determined by two variables: (i) the allowable harvest η^t , which is selected at the beginning of each year t ; and (ii) the frequency of openings, $\xi : \{1, 2, \dots, T\}$. For example, $\xi = 2$ indicates that the RA opens every two years; the total number of production years is then computed as $\frac{T}{\xi}$.

5. Results and Discussion

To guide the intuition behind our results, Table 4 shows the ecological and economic performance of the fishery for different combinations of η^ξ and ξ . The table provides a sample of ten results obtained through our simulations, including the SQ scenario (Ranking 5 in Table 4) and the optimal solution for the decision problem described in section 4.5, which corresponds to RM with $\eta^\xi = 0.3$ and $\xi = 5$ (Ranking 1 in Table 4).

Table 4. Example of the results obtained in our simulations. The optimal solution for the equation 16 is included and corresponds to the exploitation strategy receiving Ranking 1 ($\eta^\xi = 0.30$, $\xi = 5$). All results are calculated using initial densities of $d^{t=0} = 152$ immature/ha and $d^{t=0} = 115$ adults/ha, and carrying capacity of $K = 350$. All exploitation strategies are ranked according to the combination of their NPV_{40} and d outcomes.

Exploitation strategy	NPV_{40} (USD million)	Average standing density of adult conchs, d (adults/ha)	Ranking (1=most preferable, 10=less preferable)
$\eta^\xi = 0.08, \xi = 1$	18.71	205	5
$\eta^\xi = 0.15, \xi = 1$	20.88	77	10
$\eta^\xi = 0.25, \xi = 2$	22.61	94	8
$\eta^\xi = 0.30, \xi = 3$	23.86	123	7
$\eta^\xi = 0.40, \xi = 4$	24.29	128	6
$\eta^\xi = 0.30, \xi = 5$	23.64	227	1
$\eta^\xi = 0.55, \xi = 5$	21.53	97	9
$\eta^\xi = 0.40, \xi = 6$	23.16	97	2
$\eta^\xi = 0.55, \xi = 7$	23.92	167	4
$\eta^\xi = 0.60, \xi = 10$	23.11	203	3

To initialize the simulations, we used the most recent survey in the ASPC, which reported average densities of 152 immature/ha and 115 adults/ha for Alicia, Bajo Nuevo and Serrana Banks (MinAmbiente, 2018), with Serrana Bank presenting the highest densities (MinAmbiente, 2018). These density values were used as starting densities for all the simulations across the entire RA.

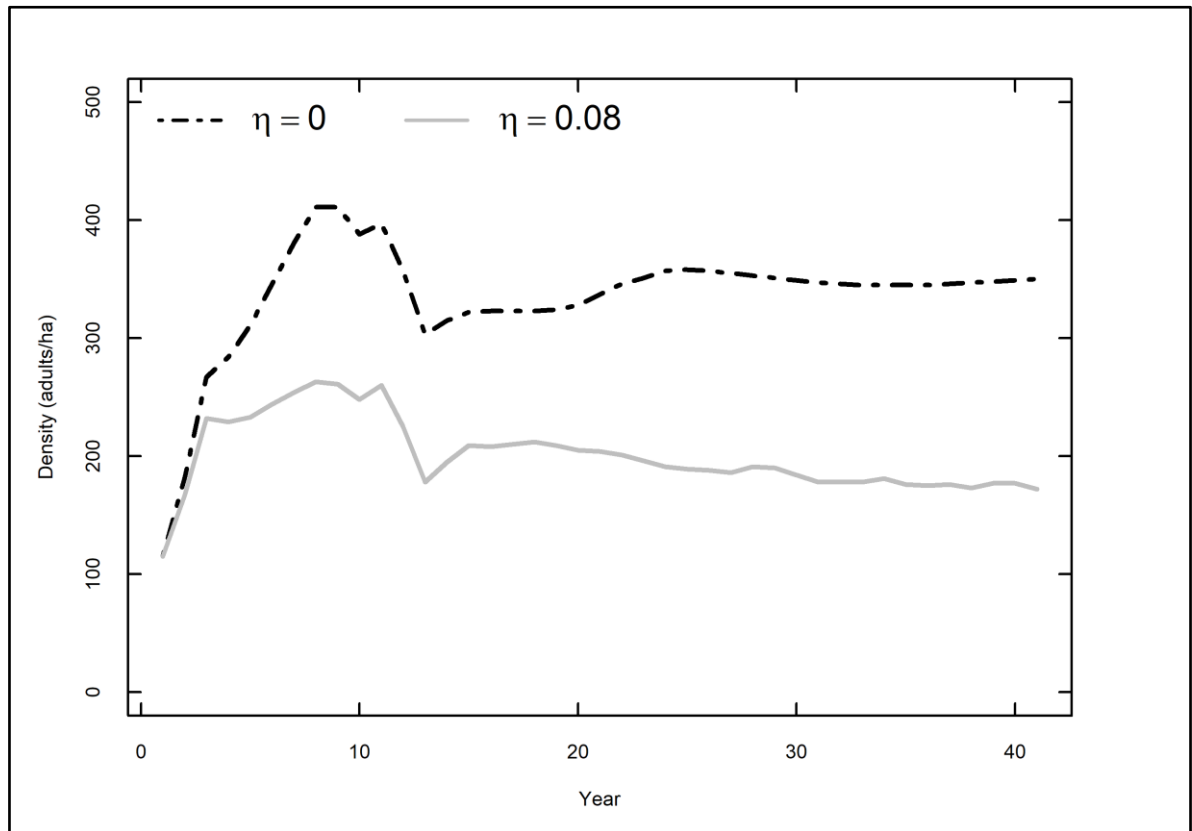
Within sustained annual harvest scenarios ($\xi = 1$), the first two rows in Table 4 illustrate the general result that allowable harvest rates above the conservation rule increase the economic performance of the fishery; however, higher harvest rates seriously undermine the sustainability of the fishery, with average standing density values usually below 100 adults/ha. Within RM scenarios ($\xi > 1$), the general result is that RM outcomes usually outperform SQ outcomes when exploitation cycles are large enough ($\xi > 4$), with η^{ξ} being significantly higher than that recommended in the conservation rule, such that $\eta^{\xi} \gg 0.08$ when $\xi > 4$. Notice that Ranking 1 in Table 4 indicates the optimal exploitation strategy for the RA but the other rankings might vary if more exploitation strategies were considered.

As a way to examine the robustness of the analysis, Monte Carlo (MC) simulations evaluated the ecological and economic performance across a range of starting densities and carrying capacities. These results are summarized in the Appendix. Next, we compare the economic and ecological outcomes obtained for two scenarios: (i) SQ, and (ii) RM with the optimal exploitation strategy.

5.1 The SQ Scenario

Population dynamics resulting from the conservation rule ($0 \leq \eta^t \leq 0.08$; equation 8) are presented in Figure 4. Notice that standing densities of adults stabilize around the carrying capacity $K = 350$ after $t = 12$ in the absence of harvest, $\eta^t = 0$.

Figure 4. Standing density of adult conchs (per ha) throughout the 40-year simulation period under the SQ scenario: (i) dynamics in the absence of fishing exploitation ($\eta^t = 0$), and (ii) dynamics resulting from the conservation rule ($0 \leq \eta^t \leq 0.08$).



Sustained annual harvest resulted in a high average standing density ($d = 205$) throughout the simulation. Standing density exceeds the starting density and the values recommended by the conservation rule. This result is consistent with the notion of the conservation rule as a reliable strategy for sustainable exploitation of conch populations. Furthermore, results suggest that fishing activity could be restored at levels similar to those observed during 2000-2004, with landings around 130mt (Figure 2). On average, the number of pearls collected each year is 625.

Table 5 summarizes the economic performance of the fishery. The NPV for the 40-year simulation period was USD 18.71 million with an average annual net revenue of USD 0.99 million. Conch meat and pearls represented 51% (USD 0.58 million) and 49% (USD 0.56 million) of average annual revenue (USD 1.14 million), respectively. Following a build-up during the first 10 years of the simulation, standing densities slowly decline from 244 to 174 adults/ha by year 40. This trend suggests that densities would stabilize below 174

adults/ha if a longer simulation period were considered. The average CPUE over the 40-year period is 37.73 kg/day/fisher. As an indicator of economic efficiency, the fishery achieves average profitability of USD 1,386 per fishing day.

Table 5. Ecological and economic performance of the QC fishery under the SQ scenario.

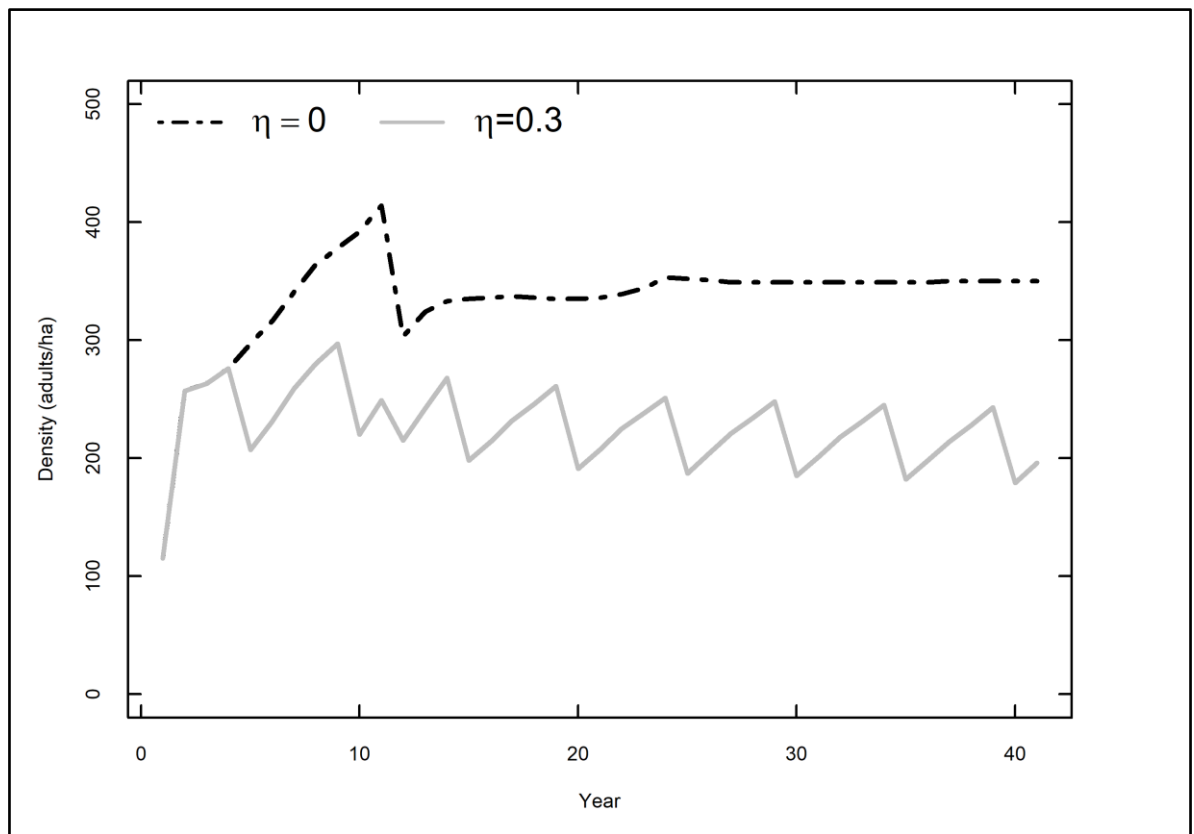
Year (t)	Density d^t (conch adults/ha)	CPUE (kg/ day/fisher)	Clean meat harvested (mt)	Number of pearls collected	Revenue (USD)	Fishing Costs (USD)	Net Revenue π^t (USD)
1	215	39.51	129.77	668	1,185,373	156,676	1,028,696
2	228	41.87	140.34	703	1,264,595	155,725	1,108,870
3	225	41.33	142.25	703	1,273,161	157,437	1,115,724
4	236	43.33	142.72	703	1,275,305	150,970	1,124,335
5	247	45.33	154.02	739	1,357,791	151,541	1,206,250
6	257	47.15	158.65	774	1,410,303	152,492	1,257,811
7	267	48.97	172.56	809	1,504,537	153,443	1,351,094
8	269	49.33	166.14	809	1,475,653	152,302	1,323,351
9	249	45.70	159.35	774	1,413,449	156,867	1,256,582
10	259	47.52	167.92	809	1,483,633	157,437	1,326,196
11	183	33.68	116.91	563	1,032,554	154,965	877,589
12	196	36.05	124.38	598	1,097,786	153,823	943,963
13	212	38.96	132.74	633	1,167,084	151,161	1,015,923
14	212	38.96	133.5	633	1,170,481	151,161	1,019,321
15	215	39.51	143.02	668	1,244,984	156,676	1,088,307
16	214	39.33	135.52	668	1,211,245	157,247	1,053,998
17	208	38.23	132.49	633	1,165,964	153,633	1,012,331
18	209	38.42	125.19	633	1,133,110	153,063	980,047
19	207	38.05	127.37	633	1,142,900	154,394	988,506
20	201	36.96	123.22	598	1,092,581	150,590	941,991
21	199	36.60	121.05	598	1,082,824	151,921	930,903
22	191	35.14	127.48	598	1,111,760	157,437	954,323
23	188	34.59	115.68	563	1,026,999	151,351	875,648
24	190	34.96	125.26	598	1,101,754	158,198	943,556
25	188	34.59	117.51	563	1,035,231	151,351	883,881
26	188	34.59	121.23	563	1,052,001	151,351	900,650
27	194	35.69	129.63	598	1,121,432	155,345	966,087
28	188	34.59	118.46	563	1,039,533	151,351	888,182
29	184	33.87	117.61	563	1,035,667	154,204	881,463
30	188	34.59	120.58	563	1,049,071	151,351	897,721
31	187	34.41	117.64	563	1,035,817	151,921	883,896
32	188	34.59	120.51	563	1,048,754	151,351	897,403
33	183	33.68	118.39	563	1,039,215	154,965	884,251
34	180	33.14	120.9	563	1,050,511	157,247	893,264
35	179	32.96	117.57	563	1,035,500	158,008	877,492
36	178	32.77	109.9	528	969,332	149,829	819,502
37	178	32.77	111.16	528	975,005	149,829	825,175
38	178	32.77	119.58	563	1,044,571	158,769	885,802
39	178	32.77	108.39	528	962,536	149,829	812,707

40	174	32.05	110.26	528	970,955	152,872	818,083
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5.2 The Optimal RM Scenario

Population dynamics under rotational harvesting are presented in Figure 5. The solution to the optimization problem in equation 16 called for $\eta^* = 0.3$ and $\xi^* = 5$, meaning that the RA is closed down from year 1 through year 4 to let biomass rebuild and is opened in year 5 at an allowable harvest rate of $\eta^t = 0.3$. Production cycles are therefore initiated in years $t : \{5, 10, 15, 20, 25, 30, 35, 40\}$ with $\eta^t = 0.3$.

Figure 5. Standing density of adult conchs (per ha) throughout the 40-year simulation period under the RM scenario: (i) dynamics in the absence of fishing exploitation ($\eta^t = 0$), and (ii) dynamics under rotational harvest management ($0 \leq \eta^t \leq 0.65$).



Average standing density was $d = 227$ (11% higher relative to SQ) throughout the simulation, which is above the values recommended by the conservation rule. Results also suggested that fishing activity could be restored at levels similar to those observed in the late

1980s (Figure 2), with landings around 759mt obtained every five years. On average, the number of pearls collected in each cycle is 4,610; this results in 922 pearls collected each year.

Table 6 summarizes the economic performance of the fishery. The NPV for the 40-year simulation period was USD 23.64 million (26% higher relative to SQ) with an average annual net revenue of USD 1.34 million (35% higher than SQ). Conch meat and pearls represented 45% (USD 0.68 million) and 55% (USD 0.83 million) of average annual net revenue (USD 1.51 million). Notice that, within optimal RM, revenues from pearls are 22% higher than revenues from conch meat. The highest net revenue was achieved in the second production cycle, with harvest taking place at year 10. Similar to the SQ scenario, maximum standing densities are achieved early in the simulation period (years 5 and 10), followed by somewhat slower densities in the subsequent production cycles. However, densities seem to stabilize by the eighth production cycle (year 40). The average CPUE over the 40-year period is 56.46 kg/day/fisher, which is 50% higher relative to the SQ scenario. In the RM scenario, the fishery achieves an average net revenue of USD 1,768 per fishing day, which is 28% higher relative to the SQ scenario.

Table 6. Ecological and economic performance of the QC fishery under the optimal RM scenario.

Year (t)	Density d^t (conch adults/ha)	CPUE (kg/ day/fisher)	Clean meat harvested (mt)	Number of pearls collected	Revenue (USD)	Fishing Costs (USD)	Net Revenue π^t (USD)
1	196	0	0	0	0	22,988	-22,988
2	243	0	0	0	0	22,988	-22,988
3	264	0	0	0	0	22,988	-22,988
4	277	0	0	0	0	22,988	-22,988
5	204	60.11	778.06	4,880	7,893,708	760,143	7,133,565
6	231	0	0	0	0	22,988	-22,988
7	252	0	0	0	0	22,988	-22,988
8	265	0	0	0	0	22,988	-22,988
9	281	0	0	0	0	22,988	-22,988
10	208	61.28	863.59	5,158	8,528,136	787,195	7,740,941
11	241	0	0	0	0	22,988	-22,988
12	262	0	0	0	0	22,988	-22,988
13	233	0	0	0	0	22,988	-22,988
14	258	0	0	0	0	22,988	-22,988
15	197	58.07	778.87	4,770	7,797,539	768,717	7,028,821
16	212	0	0	0	0	22,988	-22,988
17	229	0	0	0	0	22,988	-22,988
18	243	0	0	0	0	22,988	-22,988
19	258	0	0	0	0	22,988	-22,988
20	191	56.32	752.22	4,548	7,477,941	756,125	6,721,816
21	207	0	0	0	0	22,988	-22,988
22	224	0	0	0	0	22,988	-22,988
23	237	0	0	0	0	22,988	-22,988
24	251	0	0	0	0	22,988	-22,988
25	186	54.86	724.69	4,381	7,204,290	748,078	6,456,213
26	204	0	0	0	0	22,988	-22,988
27	221	0	0	0	0	22,988	-22,988
28	234	0	0	0	0	22,988	-22,988
29	248	0	0	0	0	22,988	-22,988
30	185	54.57	724.69	4,381	7,204,290	751,954	6,452,337
31	201	0	0	0	0	22,988	-22,988
32	218	0	0	0	0	22,988	-22,988
33	231	0	0	0	0	22,988	-22,988
34	245	0	0	0	0	22,988	-22,988
35	182	53.69	724.69	4,381	7,204,290	763,834	6,440,457
36	198	0	0	0	0	22,988	-22,988
37	214	0	0	0	0	22,988	-22,988
38	228	0	0	0	0	22,988	-22,988
39	243	0	0	0	0	22,988	-22,988

40	179	52.82	724.69	4,381	7,204,290	776,106	6,428,184
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In short, both ecological and economic indicators clearly reveal that rotational harvesting outperforms the SQ scenario.

5.3 Policy Implications

The following considerations provide further context to the results of the analysis.

(i) High recruitment rates, low mobility, and low natural mortality of conch adults suggest that sustainable harvests are possible at levels higher than those recommended in the SQ. Results also suggest that the MSY may be below the reference value implied in SQ. The conservation rule in SQ is a stock-dependent regulation that estimates $MSY = 0.08(B^t - IUU^t(I))q$; this is $\eta^t = 0.08$ subject to $d^t \geq 100$ (Medley, 2008). Our model, however, indicates $\eta^{t*} = 0.3$ subject to $d^{t*} \geq 100$ but only if harvest takes place every $\xi = 5$ years and biomass remains undisturbed during the four-year closure periods, such that $t^* = \xi t, t \in [1, T]$. Thus, t^* determines the year when fishing occurs. Given that $\left(\frac{\eta^{t*}}{\xi} = 0.06\right) < 0.08$, with all other variables being equal, MSY is on average lower in RM.

(ii) The risk of overfishing may be higher under RM in production years due to the higher allowable harvest rate η^t and the presence of IUU fishing. To address these uncertainties, scientific-based stock assessments should be carried out regularly to achieve reasonably accurate estimates of total exploitable biomass. Given the importance of the fishery to local communities, restriction of access in the form of Territorial Use Rights for Fishing (TURF) programs may contribute to reduce IUU fishing and allow local fishers to be more involved in management. TURF schemes could be co-managed by the existing cooperatives in the ASPC, contributing to more efficient allocation of resources (Cancino *et al.*, 2007; Branch, 2009; Nowlis, 2012). For example, the banishment of diving gear is a sensible conservation measure under SQ. However, eschewing diving gear may be unnecessary in a TURF context, as incentives for overfishing are attenuated by the strengthened property rights in the fishery. The reintroduction of diving gear should be accompanied by formal dive trainings and certifications, substitution of obsolete technologies, and annual equipment safety inspections, among other steps (Tewfik, 2002; Prada *et al.*, 2017). Furthermore, active restoration of conch habitats during closure periods is recommended as it may lead to increases in the productivity of the stock.

(iii) Closures and subsequent reopenings lead to an increase in economic benefits because larger conchs are harvested and a higher number of pearls is collected. However,

these benefits will only be sustained if the fishery develops an efficient traceability system meeting international standards, which is a requirement for the reactivation of conch exports. Traceability systems may also help legally harvested conch products fetch higher prices in international markets (Prada *et al.*, 2017). Certification of pearls will also be essential to ensure the legitimacy of the pearl trade and to guarantee higher incomes for fishers.

(iv) The RM scenario does not imply that all fishing grounds within the RA should shut down simultaneously. Annual harvests can be obtained through the proper rotation of fishing grounds. For example, Serrana Bank could support exploitation in year one, followed by a four-year closure period. In year two, Alicia and Bajo Nuevo Banks could be open to fishing and then closed down for the next four years, and so on for all other grounds within the RA. Future research could explore the specific details of these RM schemes.

6. Conclusions

This study recommends a thorough reexamination of the management framework that has traditionally guided exploitation of QC stocks in the Colombian Caribbean. Relative to the SQ scenario based on Medley's conservation rule, superior ecological and economic results can be obtained under a rotational harvesting scheme consisting of four-year closures followed by removal of 30% of the exploitable biomass in the fifth year. Coupled with a properly designed rights-based management framework such as a TURF program, rotational harvesting has tremendous potential to enhance conch stocks and improve fishing efficiency, as harvests would consist of larger conchs and diving gear could be reintroduced to the fishery.

Because rotational harvesting involves the periodic closure of fishing grounds, there might be opposition from local communities heavily reliant on the conch resource for their daily subsistence. The key insight to communicate to local communities and resource managers is that the long-term ecological and economic benefits created by rotational management would outweigh any initial losses in terms of forgone harvests. Investments in periodic scientific assessments of the resource would assist managers with the implementation of rotational strategies and would build greater trust among local communities.

References

- Anderson, Å. (2015). The Rarest Pearls in the World. TheJewelryEditor.com. Available at <http://www.thejewelleryeditor.com/jewellery/article/worlds-rarest-pearls-abalone-conch-melo/#:~:text=Conch%20pearls%20are%20also%20extremely,as%20much%20as%20US%24120%2C000>.
- Appeldoorn, R. S. (1988a). Ontogenetic changes in natural mortality rate of queen conch *Strombus gigas* (Mollusca: Megagastropoda). *Bulletin of Marine Science*, 42(2), 159–165.
- Appeldoorn, R. S. (1988b). Age determination, growth, mortality and age of first reproduction in adult queen conch, *Strombus gigas* L., off Puerto Rico. *Fish Research*, 6, 363–378.
- Appeldoorn, R. S. (1993). Reproduction, spawning potential ratio and larval abundance of queen conch off La Parguera, Puerto Rico. Submitted to CFMC, Hato Rey PR. 25 pp.
- Appeldoorn, R. S. (1994). Spatial variability in the morphology of queen conch and its implications for management regulations. Pages 145-157 in: RS Appeldoorn and B Rodriguez (eds.) Queen conch biology, fisheries, and mariculture. Fundación Científica Los Roques, Caracas, Venezuela.
- Appeldoorn, R. S. (1997). Deep Water Spatial Variability in the morphology of Queen Conch and its implication for management regulations. in: CFRAMP (ed.) Lobster and Conch subproject specification and training workshop. 9 to 12 October 1995, Kingston, Jamaica. CARICOM Fishery (Research Document No 19).
- Appeldoorn, R. S., Arango, L., Cabeza, F., Castro, E. R., Glazer, R., Marshak, T., and Peñaloza, G. (2003). Queen conch distribution and population assessment of the northern banks of the San Andres Archipelago, Colombia. Final report of the Northern expedition. CORALINA - The Ocean Conservancy. San Andrés. 27 pp.
- Appeldoorn, R. S., Castro E., Glazer, R., and Prada, M. (2011). Applying EBM to queen conch fisheries in the Caribbean. Pages 177-186 in: L. Fanning, R. Mahon and P. McConney (eds.). Towards Marine Ecosystem-based Management in the Caribbean.
- Appeldoorn, R. S., and Baker, N. (2013). A Literature Review of the Queen Conch (*Strombus Gigas*). Department of Marine Sciences, University of Puerto Rico. 80 pp.

- Asche, F., Garlock, T. M., Anderson, J. L., Bush, S. R., Smith, M. D., Anderson, C. M., et al. (2018). Three pillars of sustainability in fisheries. *Proceedings of the National Academy of Sciences*, *115*(44), 11221–11225; doi: 10.1073/pnas.1807677115.
- Branch, T. A. (2009). How do individual transferable quotas affect marine ecosystems? *Fish and Fisheries*, *10*, 39–57.
- Caddy, J. F. (1993). Background concepts for a rotating harvesting strategy with particular reference to the Mediterranean red coral, *Corallium rubrum*. *Marine Fisheries Review*, *55*, 10–18.
- Campbell, A., Harbo, R. M., and Hand C. M. (1998). Harvesting and distribution of Pacific geoduck clams, *panopea abrupt*, in British Columbia. *Canadian Special Publication of Fisheries and Aquatic Sciences*, *125*, 349–358.
- Cancino, J., Uchida, H., and Wilen. J. E. (2007). TURFs and ITQs: Coordinated vs. decentralized decision making. *Marine Resource Economics*, *22*, 391–406.
- CFMC (Caribbean Fishery Management Council). (1999). Report on the queen conch stock assessment and management workshop. CFMC, Belize City, Belize.
- CITES (Convention on International Trade in Endangered Species). (2019). Convention on International Trade in Endangered Species of Wild Fauna and Flora Trade Database. Data taken from: <https://trade.cites.org/>.
- Christie, P. (2004). Marine protected areas as biological successes and social failures in southeast Asia J.B. Shipley (Ed.), *Aquatic Protected Areas as Fisheries Management Tools*, 155–164.
- Clark, C. W., and Munro, G. R. (1980). Fisheries and the processing sector: Some implications for management policy. *The Bell Journal of Economics*, *11*(2), 603–616.
- Cohen, P. J., Cinner, J. E., and Foale, S. (2013). Fishing dynamics associated with periodically harvested marine closures. *Global Environmental Change*, *23*(6), 1702–1713, ISSN 0959-3780.
- Costello, C., Ovando, D., Clavelle, T., Strauss, C. K., Hilborn, R., Melnychuk, M. C. Branch, T. A., et al. (2016). Global fishery prospects under contrasting management regimes. *Proceedings of the National Academy of Sciences*, *113*(18), 5125–5129; doi: 10.1073/pnas.1520420113.

- DANE. (2020). [In Spanish] Inflación total y meta. Departamento Administrativo Nacional de Estadística (DANE) en Colombia. Banco de la República. Data taken from: <https://www.banrep.gov.co/es/estadisticas/inflacion-total-y-meta>.
- Davis, M. (2000). Queen conch (*Strombus gigas*) culture techniques for research, stock enhancement and growout markets. In: Fingerman M, Nagabhushanam R, eds. Recent Advances in Marine Biotechnology, Volume 4 Aquaculture, Part A Seaweeds and Invertebrates. EnfieldNH: Science Publishers, Inc. pp 27–59.
- Drake, J. M., and Kramer, A. M. (2011). Allee effects. *Nature Education Knowledge*, 3(10), 2.
- Ehrhardt, N. M., and Valle-Esquivel, M. (2008). Conch (*Strombus gigas*) stock assessment manual. CFMC. San Juan PR. 128 pp.
- Foale, S. J., and Manele, B. (2004). Social and political barriers to the use of Marine Protected Areas for conservation and fishery management in Melanesia. *Asia Pacific Viewpoint*, 45, 373–386.
- Gallo-Nieto, et al. (1996). [In Spanish] Evaluación de la pesquería del caracol pala (*Strombus gigas*) y la langosta espinosa (*Panulirus spp.*) en el Departamento Archipiélago de San Andrés, Providencia y Santa Catalina (Caribe colombiano). Mem. de Resúmenes del X Sem. Nal. Cienc. y Tecnol. del Mar, CCO / COLCIENCIAS. Santafé de Bogotá (Colombia), Oct. 28-31.
- Gordon, H. (1954). The economic theory of a common property resource: The fishery, *Journal of Political Economics*, 62(2), 124–142.
- Hart, D. R. (2002). Yield- and biomass-per-recruit analysis for rotational fisheries, with an application to the Atlantic sea scallop (*Placopecten magellanicus*). *Fishery Bulletin*, 101, 44–57.
- Hebert, K. P. (2012). Southeast Alaska sea cucumber stock assessment surveys in 2011. Alaska Department of Fish and Game, Fishery Data Series No. 12–26, Anchorage.
- Heizer, S. (1993). “Knob cod”-management of the commercial sea cucumber fishery in British Columbia. *Journal of Shellfish Research*, 12, 144–145.
- Hernández-Barrero, et al. (1997a). [In Spanish] Crecimiento, mortalidad y estado de explotación del caracol pala (*Strombus gigas*, Linnaeus 1758) en el Archipiélago de San Bernardo (Caribe colombiano). *INPA-Bol. Cientif.*, 5, 127–142.

- Hernández-Barrero, *et al.* (1997b.) [In Spanish] Captura, rendimiento y algunos aspectos socioeconómicos de la pesquería del caracol pala (*Strombus gigas*, Linnaeus 1758) en el Archipiélago de San Bernardo (Caribe colombiano). *INPA-Bol. Cientif.*, 5, 143–158.
- Hilborn, R., and Walters, C. J. (1992). Quantitative fisheries stock assessment, choice, dynamics and uncertainty. Chapman and Hall, London, 570 pp. doi:10.1007/978-1-4615-3598-0.
- Lagos-Bayona, A. L. (1994). [In Spanish] Algunos aspectos biológicos y pesqueros del caracol pala *Strombus gigas* Linnaeus, 1758 (Mollusca: Gastropoda: Strombidae), en el Archipiélago de San Bernardo y ensayos sobre su cultivo en laboratorio: Tesis, Univ. de Bogotá Jorge Tadeo Lozano, Fac. Biol. Marina. 154 pp.
- Lai, H., and Bradbury, A. (1998). A modified catch-at-size analysis model for a red sea urchin (*Strongylocentrotus fanciscanus*) population. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 125, 85–96.
- Márquez-Petrelt, E. (1993). [In Spanish] Biología poblacional del caracol pala *Strombus gigas* Linnaeus, 1758 en las Islas de Providencia y Santa Catalina: Tesis, Univ. de Bogotá Jorge Tadeo Lozano, *Fac. Biology Marina*, 102.
- Márquez-Petrelt, E., and Dávila-Vila, E. O. (1994). [In Spanish] Dinámica poblacional y pesquera del caracol pala *Strombus gigas* Linnaeus, 1758 en las Islas de Providencia y Santa Catalina, Tomo 2 pp. 374-383 (in) Mem. De Resúm. del IX Sem. Nal. Cienc. y Tecnol. del Mar y II Congr. Lat.-Amer. En Cienc. del Mar, CCO / EAFIT. Medellín (Ant.) Colombia, Nov. 21–25.
- Márquez-Petrelt, E., Dávila-Vila, E. O., and Gallo-Nieta, J. (1994). [In Spanish] Dinámica poblacional y pesquera del caracol pala *Strombus gigas* Linnaeus, 1758 en las Islas de Providencia y Santa Catalina. *INPA-Bol. Cientif.*, 2, 110–123.
- Marshak, A. R., Appeldoorn, R. S., and Jimenez, N. (2006). Utilization of GIS Mapping in the measurement of the spatial distribution of queen conch *Strombus gigas* in Puerto Rico. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 57, 31–48.
- Medley, P. (2008). Monitoring and managing queen conch fisheries: a manual. FAO (Fisheries Technical Paper No. 514). FAO, Rome. 2008.
- MinAmbiente. (2018). [In Spanish] Plan de Acción Nacional para la Conservación y Manejo del Caracol Pala (*Strombus gigas*, Linnaeus, 1758) en el Caribe Colombiano (PAN-

- CARACOL COLOMBIA). Ministry of Environment, Government of Colombia, 45 pp.
- Mora, O. (1994). [In Spanish] Análisis de pesquería de caracol pala (*Strombus gigas* L.) en Colombia. pp 137-144 (in) Appeldoorn, R., S., and Rodriguez, R. (eds.) Queen conch biology, fisheries, and mariculture. Fundación Científica Los Roques, Caracas, Venezuela.
- Myers, R. A., Fuller, S. D., and Kehler, D. G. (2000). A fisheries management strategy robust to ignorance: Rotational harvest in the presence of indirect fishing mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 2357–2362.
- NMFS. (2020). Commercial Fisheries Statistics. National Marine Fisheries Service, Fisheries Statistics and Economic Division. Data taken from: <https://www.st.nmfs.noaa.gov/commercial-fisheries/foreign-trade/applications/annual-trade-balance-for-product>.
- Nowlis, J., and Van Benthem, A. A. (2012). Do property rights lead to sustainable catch increases? *Marine Resource Economics*, 27, 89–105.
- Ortegón-Guasca, O. A. (2006). [In Spanish] Perla del caracol pala *Strombus gigas* (Linnaeus, 1758): Apariciones y primer ensayo de su formación, Caribe colombiano. Trabajo de grado para optar al título de Biólogo Marino. Universidad de Bogotá Jorge Tadeo Lozano. 179 pp.
- Pfister, C. A., and Bradbury, A. (1996). Harvesting red sea urchins: Recent effects and future predictions. *Ecological Applications*, 6, 298–310.
- Phillips, A. C., and Boutillier, J. A. (1998). Stock assessment and quota options for the sea cucumber fishery. In B. J. Waddell, G. E. Gillespie, and L. C. Wlathers (eds.). Invertebrate Working Papers reviewed by the Pacific Stock Assessment Review Committee (PSARC) in 1995. Part 2. Echinoderms Can Tech Re. *Fish Aquatic Science*, 2215, 147–167.
- Plagányi, E. A., Skewes, T., Murphy, N., Pascual, R., and Fischer, M. (2015). Crop rotations in the sea: Increasing returns and reducing risk of collapse in sea cucumber fisheries *Proceedings of the National Academy of Sciences May 2015*, 112(21), 6760–6765; DOI: 10.1073/pnas.1406689112.
- Posada, J. M., Garcia-Moliner, G., and Oliveras, I. N. (1997). Proceedings of the International Queen Conch Conference. CFMC. San Juan Puerto Rico. 160 pp.

- Prada, M. C., Castro, E., Taylor, E., Puentes, V., Appeldoorn, R. S., and Daves, N. (2009). Non-Detriment findings for the Queen Conch in Colombia. NOAA Fisheries-Blue Dream Ltd (Eds.). San Andres Island, Colombia, 51 pp.
- Prada, M. C., Appeldoorn, R. S., Van Eijs, S., and Pérez, M. M. (2017). Regional Queen Conch Fisheries Management and Conservation Plan. (FAO Fisheries and Aquaculture Technical Paper No. 610). Rome, FAO. 70 pp.
- Randall, J. E. (1964). Contribution to the biology of the Queen conch *Strombus gigas*. *Bulletin of Marine Science*, 14, 246–295.
- Sluczanowski, P. R. (1984). A management-oriented model of an abalone fishery whose sub stocks are subject to pulse fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, 41, 1008–1014.
- Smikle, S. G. (2010). Pedro Bank queen conch fishery, assessment and TAC recommendation. Unpublished report of the Fisheries Division of Jamaica, Ministry of Agriculture.
- Spade, D. J., Griffitt, R. J., Liu, L., Brown-Peterson, N. J., Kroll, K. J., et al. (2010). Queen Conch (*Strombus gigas*) testis regresses during the reproductive season at Nearshore sites in the Florida Keys. *PLOS ONE*, 5(9), e12737. <https://doi.org/10.1371/journal.pone.0012737>.
- Stoner, A. W. (1989). Winter mass migration of juvenile queen conch *Strombus gigas* and their influence on the benthic environment. *Marine Ecology Progress Series*, 56, 99–104.
- Stoner, A. W. and Schwarte, K. C. (1994). Queen conch, *Strombus gigas*, reproductive stocks in the central Bahamas: Distribution and probable sources. *Fishery Bulletin*. 92, 171–179.
- Stoner, A. W., Ray, M., and Waite, J. M. (1995). Effects of a large herbivorous gastropod on macrofauna communities in tropical seagrass meadows. *Marine Ecological Progress Series*, 121, 125–137.
- Stoner, A. W., and Ray-Culp, M. (2000). Evidence for Allee effects in an overharvested marine gastropod: Density dependent mating and egg production. *Marine Ecology Progress Series*, 202, 297–302.

- Stoner, A. W., Davis, M., and Booker, C. (2011). Surveys of queen conch populations and reproductive biology at Lee Stocking Island and the Exuma Cays Land and Sea Park, the Bahamas. Bahamas, Community Conch.
- Stoner A. W., Mueller, K. W., Brown-Petersen, N. J., Davis, M. H., and Booker, C. J. (2012). Maturation and age in queen conch *Strombus gigas*: Urgent need for changes in harvest criteria. *Fisheries Research*, 131–133, 76–84.
- Taylor, E., Baine, M., Killmer, A., and Howard, M. (2013). Seaflower marine protected area: Governance for sustainable development. *Marine Policy*, 41, 57–64.
- Tewfik, A. (2002). Regional overview of queen conch (*Strombus gigas*) resources in CARICOM/ CARIFORUM countries.
- Torres-Rosado, Z. A. (1987). Distribution of two meso gastropods, the queen conch, *Strombus gigas* Linnaeus, and the milk conch, *Strombus costatus* Gmelin, in La Parguera, Lajas, Puerto Rico. MS Thesis, UPR, Mayagüez Campus. 37 pp.
- Valderrama, D., and Anderson, J. (2007). Improving utilization of the Atlantic Sea Scallop resource: An analysis of rotational management of fishing grounds. *Land Economics*, 83(1), 86–103. <http://www.jstor.org/stable/27647749>.
- Walters, C. J., and Martell, S. J. D. (2004). *Fisheries Ecology and Management*. Princeton and Oxford: Princeton University Press.
- Weil, E., and Laughlin, R. (1984). The biology, population dynamics and reproduction of the queen conch *Strombus gigas* L., in the Archipelago Los Roques National Park. *Journal of Shellfish Research*, 491, 45–62.

Appendix

To analyze the effects of variation in starting densities and carrying capacity on ecological and economic performance, we conducted a series of MC simulations. The MC simulations were used to compare average standing densities (ecological performance) and NPV (economic performance) over the T-year period. We use $T = 40$ years as period length for simulations (Table 2). Each MC simulation was conducted for 300 trials (Valderrama and Anderson, 2007). Without loss of insight, we assume that starting densities of immature

conchs and conch adults are identical, such that $\frac{\sum_{a=1}^2 n_a^{t=1}}{S} = \frac{\sum_{a=3}^A n_a^{t=1}}{S}$.

Each trial generates values of carrying capacity around three reference levels: $K = 200$ (low level), $K = 350$ (mid-high level), and $K = 400$ (high level). The selected RM scenario for the MC simulations is characterized by $\eta^{\xi} = 0.3$ and $\xi = 5$; it corresponds to the optimal solution of equation 16.

A.1 Effects of Variation in Starting Densities and Carrying Capacity on Ecological Performance.

Results from the MC simulations are summarized in Table A1. The results are qualitatively the same as those obtained in the main text: the highest standing density values are achieved in RM. Table A1 also shows that RM always performs better than SQ, and that differences in ecological performance increase as starting densities decrease or the carrying capacity increases. On average, RM performs 15%, 11%, and 7% better than SQ when starting densities fall between $d^{t=0} \in [50,100)$, $d^{t=0} \in [100,150)$, and $d^{t=0} \in [150,200)$, respectively. Analogously, RM performs on average 9%, 10%, and 11% better than SQ when the carrying capacity is around $K = 200$, $K = 300$, and $K = 400$, respectively. In summary, the results shown in Table A1 suggest that RM will generate higher long-term ecological benefits for the QC fishery as compared with SQ. In all cases, the average standing densities were above the tipping point of 50 adults/hectare (Minimum Stock Threshold).

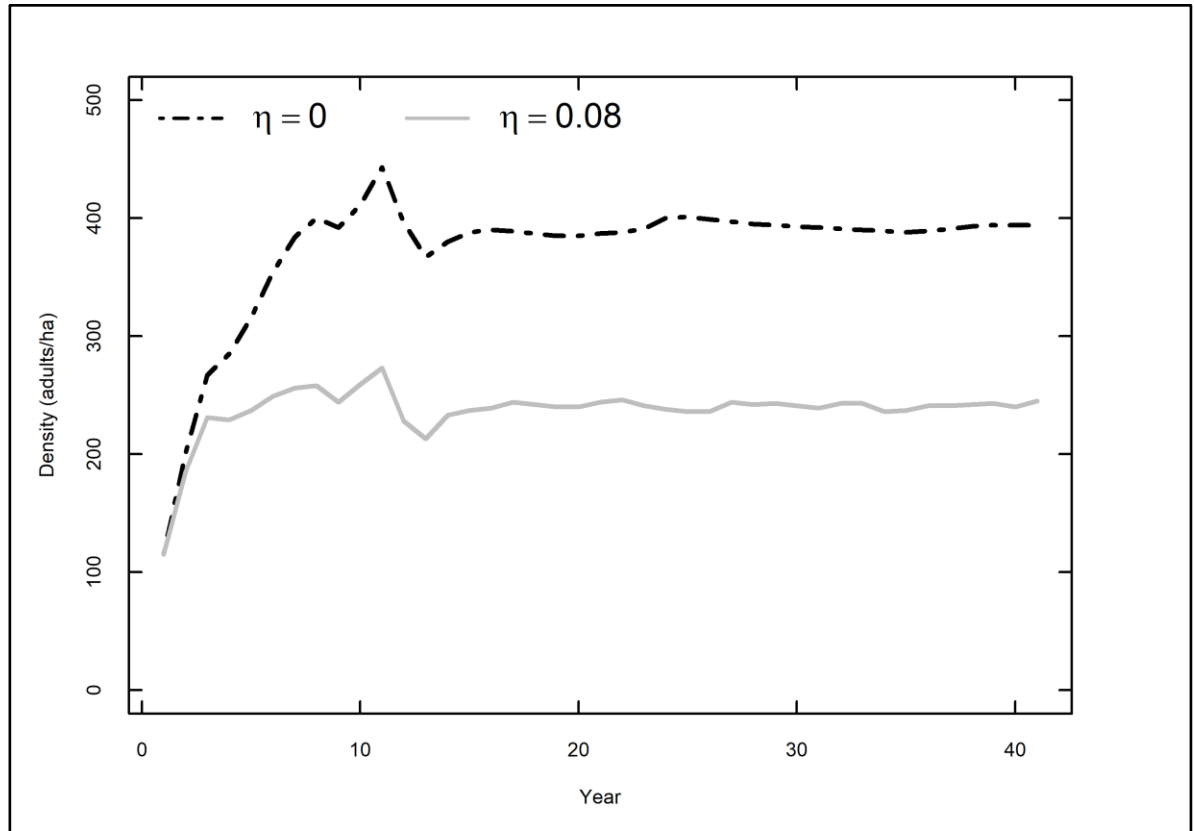
Table A1. Mean and standard deviation (in parentheses) of standing density (adults/ha) for the QC fishery resulting from Monte Carlo simulations (300 trials) across a range of starting densities and carrying capacities. $T = 40$ years.

Starting densities ($d^{t=0}$), Carrying capacity (K)	SQ scenario			RM scenario ($\eta^\xi = 0.3, \xi = 5$)		
	$K = 200$	$K = 350$	$K = 400$	$K = 200$	$K = 350$	$K = 400$
$d^{t=0} \in [50,100)$	89.40 (13.28)	126.12 (25.21)	144.04 (31.27)	100.14 (16.18)	142.2 (27.95)	170.54 (34.81)
$d^{t=0} \in [100,150)$	125.86 (7.91)	194.40 (15.06)	226.92 (16.79)	139.02 (7.36)	215.56 (13.31)	252.86 (15.16)
$d^{t=0} \in [150,200)$	142.69 (2.18)	225.59 (5.47)	265.47 (7.20)	152.37 (1.31)	243.67 (4.99)	284.08 (6.01)

In SQ, standing densities of conch adults stabilize around $d = 227$ values after the year 12 when carrying capacity is around $K = 400$ (high level) values. In Figure A1, we present an example of this result when starting densities were in between $d^{t=0} \in [100,150)$.

Different starting densities do not affect the results. In contrast, standing densities of conch adults do not stabilize over the 40-year period when carrying capacity falls below 400 adults/hectare. See Figure 4 in the main text for comparisons.

Figure A1. Standing density of conchs (per ha) throughout the 40-year simulation period under the SQ scenario, assuming a high carrying capacity ($K = 400$ adults/ha) and $d^{t=0} \in [100,150)$: (i) dynamics in the absence of fishing exploitation ($\eta^t = 0$), and (ii) dynamics resulting from the conservation rule ($0 \leq \eta^t \leq 0.08$).



A.2 Effects of Variation in Starting Densities and Carrying capacity on Economic Performance.

Results from the MC simulations are summarized in Table A2. The results are qualitatively the same as those obtained in the main text: the highest NPV is achieved in RM. Table A2 also shows that RM always performs better than SQ, and that differences in economic performance increase as starting densities and/or carrying capacity decrease. On average, RM performs 52%, 35%, and 25% better than SQ when starting densities fall between $d^{t=0} \in [50,100)$, $d^{t=0} \in [100,150)$, and $d^{t=0} \in [150,200)$, respectively. Analogously, RM performs on average 30%, 37%, and 36% better than SQ when the carrying capacity is around $K = 200$, $K = 300$, and $K = 400$, respectively. In summary, the results shown in Table A2 suggest that RM can generate higher long-term economic benefits for the QC fishery as compared with SQ.

Table A2. Mean and standard deviation (in parentheses) of NPV_{40} (USD million) for the QC fishery resulting from Monte Carlo simulations (300 trials) across a range of starting densities and carrying capacities. $T = 40$ years.

Starting densities ($d^{t=0}$), Carrying capacity (K)	SQ scenario			RM scenario ($\eta^\xi = 0.3, \xi = 5$)		
	$K = 200$	$K = 350$	$K = 400$	$K = 200$	$K = 350$	$K = 400$
$d^{t=1} \in [50,100)$	5.10 (2.16)	8.37 (2.67)	9.81 (3.05)	7.83 (2.23)	12.57 (3.59)	15.01 (4.37)
$d^{t=0} \in [100,150)$	10.64 (1.21)	16.20 (1.84)	19.28 (2.21)	13.68 (1.24)	22.30 (2.01)	26.22 (2.30)
$d^{t=0} \in [150,200)$	13.48 (0.54)	20.76 (0.97)	24.72 (1.13)	16.28 (0.35)	27.07 (0.92)	31.72 (1.14)