



REVIEW

Integrating population biology into conservation management for endangered Nassau grouper *Epinephelus striatus*

Krista D. Sherman^{1,2}, Craig P. Dahlgren², Jamie R. Stevens¹, Charles R. Tyler^{1,*}

¹Biosciences, Geoffrey Pope Building, University of Exeter, Stocker Road, Exeter, Devon EX4 4QD, UK

²Science and Policy, Bahamas National Trust (BNT), PO Box N-4105, Nassau, Bahamas

ABSTRACT: Groupers are a phylogenetically diverse group and include many ecologically and economically valuable predatory marine fishes that have experienced drastic population declines. Reproduction via spawning aggregations increases the vulnerability of grouper species such as Nassau grouper *Epinephelus striatus* to overfishing, and this is likely to be a major contributing factor to population declines. However, the lack of information pertaining to population structure and dynamics of Nassau grouper spawning aggregations has impeded effective ecosystem-based fisheries management for remaining stocks. Worldwide, The Bahamas has the largest number of known Nassau grouper spawning aggregations, yet very little is known about the overall status of groupers in the region. Landings of Nassau grouper in The Bahamas have declined by 86 % in the last 20 years from a peak of 514 t in 1997. Available data suggest that existing management measures are failing in their attempts to prevent further declines. Effective management strategies are urgently needed that balance ecological and socioeconomic considerations to enable a sustainable Nassau grouper fishery. This review provides an analysis of the reproductive and population biology of Nassau grouper and a suggested framework to direct future research efforts for enhancing conservation management of this endangered marine fish species.

KEY WORDS: Fisheries management · Population structure · Marine protected area · MPA · Spawning aggregation · Genetic diversity · Microsatellite · Single nucleotide polymorphisms

INTRODUCTION

Spawning aggregations—where conspecific fish come together in high densities to release their gametes (eggs and sperm) into the water or onto a suitable substrate—occur in over 100 reef fish species (Sadovy de Mitcheson & Colin 2012, Russell et al. 2014), many of which have economic importance, including parrotfish (Scaridae), groupers (Epinephelidae) and snappers (Lutjanidae) (Heemstra & Randall 1993, Beets & Hixon 1994, Colin 1996, Morris et al. 2000, Sadovy de Mitcheson et al. 2008, Coleman et al. 2010, Craig et al. 2011, Choat 2012, Colin 2012). The existence of these spawning aggregations is

threatened by a range of environmental and anthropogenic pressures, including overfishing (Sadovy de Mitcheson & Erisman 2012, Robinson et al. 2014), habitat loss and degradation (Robinson & Samoilys 2013), invasive species (Muñoz et al. 2011) and climate change (Cheung et al. 2012). According to a recent report, 26 % of aggregating marine fish species have decreased, 4 % have disappeared and the status of most other aggregating fish populations are unknown (Russell et al. 2014).

Groupers belonging to the family Epinephelidae are a phylogenetically diverse group of predatory fishes comprising 6 subfamilies, 12 genera and 163 species that inhabit a wide range of marine habitats

*Corresponding author: C.R.Tyler@exeter.ac.uk

(Baldwin & Johnson 1993, Heemstra & Randall 1993, Craig & Hastings 2007, Craig et al. 2011, Schoelincx et al. 2014). Fishes from the genus *Epinephelus* are paraphyletic, with larger bodied species sharing a common ancestry despite a geographic discontinuity between the Atlantic and Eastern Pacific (Craig & Hastings 2007). Groupers from the subfamily Epinephelinae are found throughout subtropical and tropical oceans and account for a substantial percentage (~12%) of annual global fisheries revenue, particularly in Asia via the live fish trade and aquaculture, and in developing Caribbean countries via commercial, recreational and subsistence fisheries (Buchan 2000, Rudd & Tupper 2002, Craig et al. 2011, Sadovy de Mitcheson et al. 2013, FAO 2014, Western Central Atlantic Fishery Commission 2014). In Asia, a consistently high demand for groupers has driven prices up to US\$100 kg⁻¹ (FAO 2014). Globally, grouper stocks have declined by around 60% over the last 3 decades (Sadovy de Mitcheson et al. 2008, Sadovy de Mitcheson & Colin 2012), with some even greater regional and local population declines (Cheung et al. 2013, C. P. Dahlgren et al. unpubl. data). These declines are believed to be due to a combination of grouper life history characteristics and unsustainable fishing practices. Many of the larger grouper species are *K*-selected strategists with long life-spans, slow growth rates and delayed sexual maturity (Coleman et al. 1996, 2000, Sadovy de Mitcheson & Colin 2012). For many grouper species, much of the exploitation occurs at spawning aggregation sites, which increases their susceptibility to over-exploitation (Heemstra & Randall 1993, Musick 1999, Coleman et al. 2000, Morris et al. 2000, Sadovy de Mitcheson et al. 2013). Overfishing of grouper may lead to alterations in the structure of spawning aggregations (Carter et al. 1991, Sadovy & Domeier 2005, Sadovy de Mitcheson & Colin 2012), and this in turn may impact negatively on long-term reproductive success.

Recognition of the vulnerability of grouper stocks has led to conservation efforts to evaluate the status of populations to help prevent further declines at both regional and global scales. Of the grouper species assessed to date, the International Union for the Conservation of Nature (IUCN) Grouper and Wrasses Specialist Group has classified 13% as threatened (i.e. critically endangered, endangered or vulnerable) and 14% as near threatened. For approximately 30%, there are insufficient data to make any valued judgement on their status (IUCN 2015). The lack of species-specific information pertaining to population structure and dynamics of spawning aggregations

is one of the major impediments for effective ecosystem-based fisheries management for remaining grouper stocks.

Nassau grouper *Epinephelus striatus* (Bloch 1792), one of the most important grouper species economically, form annual transient fish spawning aggregations (FSAs; Domeier 2012). This is when a group of conspecific fish gathers at a site located at a considerable distance outside their home range for the purpose of spawning. At these sites, fish densities are greater than those outside of the aggregation area and often represent the total reproductive effort for participating individuals (Domeier 2012). Up to 100 000 Nassau grouper have been observed in a single spawning aggregation off Cat Cay, Bimini in The Bahamas (Smith 1972).

Sixty to eighty Nassau grouper spawning aggregation sites have been identified globally (Sadovy & Eklund 1999), but many of these have been lost due to overfishing (Sadovy de Mitcheson et al. 2008). The Bahamas has the largest number (ca. 30 sites) of known viable (reproductively active) Nassau grouper spawning aggregations (Sadovy & Eklund 1999, Cheung et al. 2013; Fig. 1), but with significant declines apparent at many of the historic aggregation sites (e.g. Cat Cay, Bimini and High Cay, Andros). However, sighting frequencies and densities of Nassau grouper are still 2 to 3 times higher in The Bahamas relative to other parts of the Caribbean (Stallings 2009, Dahlgren et al. 2016). For this region in particular, there is an urgent need to better understand the reproductive biology and evaluate the status of remaining grouper stocks to strengthen and inform national and regional management strategies. Cheung et al. (2013) reported that local fishers have recognised decreases in abundance and sizes of Nassau grouper caught at spawning aggregation sites since the 1990s, and the majority (82%) were concerned about the long-term viability of the fishery. If Nassau grouper populations continue to be overfished at their current rate (Cheung et al. 2013), this will likely result in the collapse of the fishery within the next few decades, with very considerable economic and social ramifications for The Bahamas and the wider Caribbean. As a highly prized commercial fish species, the Nassau grouper is very important to the livelihoods of thousands of fishermen in The Bahamas (Buchan 2000, Cushion & Sullivan-Sealey 2008). It is imperative, therefore, that management plans balance ecological and socioeconomic considerations to ensure a sustainable Nassau grouper fishery. This review provides an analysis of the reproductive and population biology of Nassau grouper with

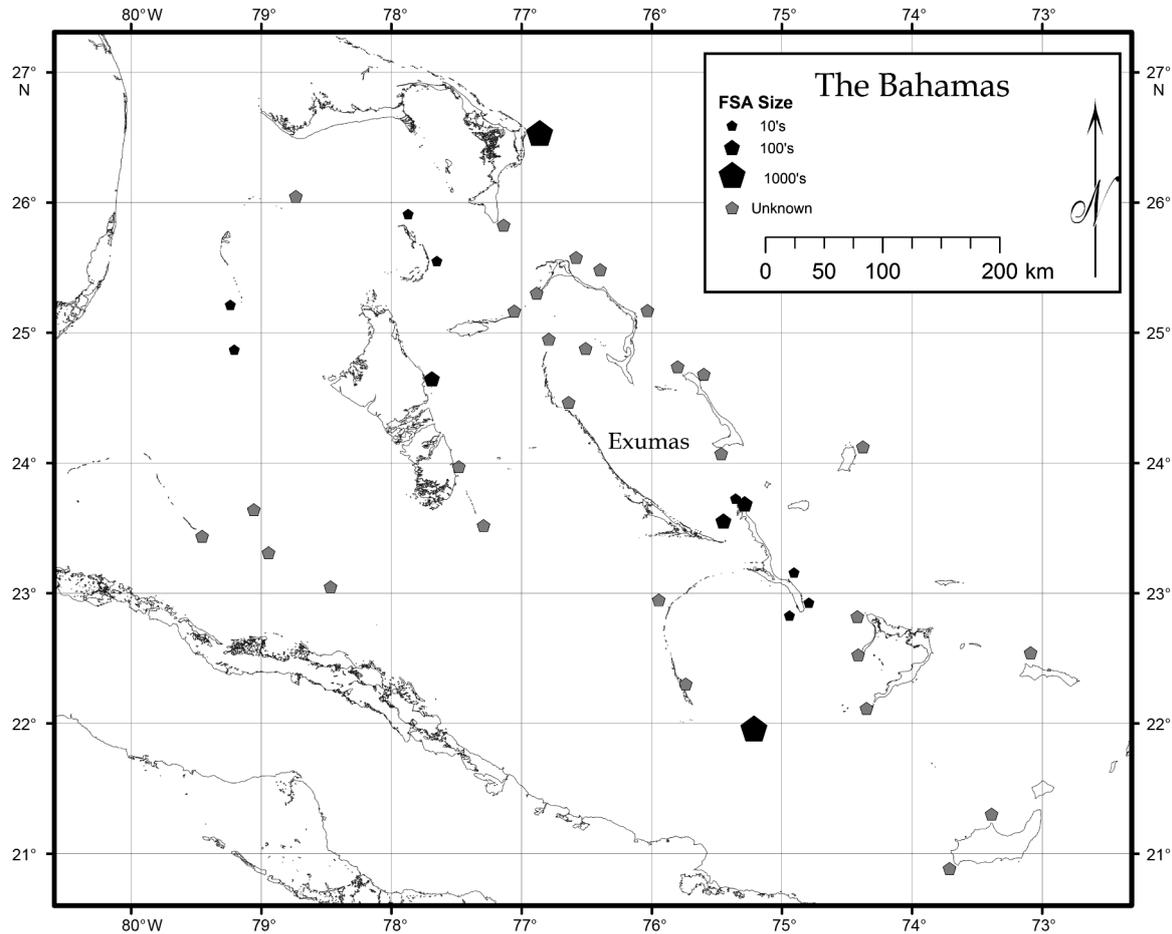


Fig. 1. Approximate locations of known and anecdotal Nassau grouper *Epinephelus striatus* fish spawning aggregations (FSAs) in the Bahamian archipelago. Spawning aggregation sites are denoted by black pentagons of various sizes corresponding to estimates of Nassau grouper abundance: small = 10's of fish, medium = 100's of fish, large = 1000's of fish. Grey pentagons = unknown (i.e. no *in situ* data or unverified spawning aggregation site). Figure based on the most recent data available from each site

a view to help support and direct future research efforts and approaches for enhancing conservation management of this endangered marine fish species.

BASIC BIOLOGY AND ECOLOGY

Nassau grouper, subfamily Epinephelinae, are slow growing, relatively long-lived (ca. 30 yr) predatory fish growing up to a maximum weight of 27 kg (Albins et al. 2009, Froese & Pauly 2014) that inhabit nearshore habitats up to 255 m in depth throughout the tropical Western Atlantic, Caribbean Sea and parts of the Gulf of Mexico (Starr et al. 2007, Albins et al. 2009, Froese & Pauly 2014). Normally Nassau grouper are light grey or olive to reddish brown in colour, with 5 distinct dark bars along the body, but they may undergo rapid colour and pattern changes that are associated with various behaviours (Archer

et al. 2012, Watson et al. 2014). Nassau grouper exhibit dietary shifts during ontogeny. As larvae and pelagic juveniles, they consume primarily zooplankton and copepods (Grover et al. 1998); as demersal juveniles in nearshore benthic habitats (i.e. mangroves, seagrasses and macroalgal clumps), they feed mainly on crustaceans (Eggleston 1995, Eggleston et al. 1998, Grover et al. 1998, Dahlgren & Eggleston 2001, Dahlgren et al. 2006); as late juveniles or sub-adults living on hard bottom and patch reefs, they consume both invertebrates and fish (Dahlgren & Eggleston 2000, Camp et al. 2013); and as adults, living in deeper and more rugose reef habitats, they predominantly feed on fish (Eggleston et al. 1998). The timing of these ontogenetic shifts is mediated by a combination of predator-prey dynamics, ecophysiological processes and habitat suitability (Dahlgren & Eggleston 2001, Young et al. 2006, Semmens et al. 2008, Stallings 2008, Camp et al. 2013).

Major loss of any of the habitats utilised by groupers during ontogeny is likely to influence their abundance and survival. Perhaps the greatest habitat losses influencing grouper populations arise from alterations or destruction of nearshore nursery areas, including mangroves and seagrasses, and by the declining state of coral reef systems (Dahlgren & Eggleston 2001, Gardner et al. 2003, Lotze et al. 2006, Semmens et al. 2008). Ellis et al. (1997) demonstrated that changes in water temperature experienced by early life stages of Nassau grouper may have profound effects on their food consumption, development and growth rate, and these factors may play a significant role in the annual fluctuations in the survival of this species. This may be compounded by the fact that these early life stages already experience high mortality rates due primarily to predation (Choat 2012) and disease susceptibility (Harikrishnan et al. 2011). Sea temperature may also affect adult grouper directly by affecting metabolism, reproduction, growth and behaviour (Colin 1992, Watanabe et al. 1995b). Other environmental stressors that are likely to affect grouper survival directly include predicted climate-related changes in ocean chemistry (e.g. ocean acidification) (Young et al. 2006, Semmens et al. 2008, Cheung et al. 2012, Sunday et al. 2014). However, to date, very little research has been done examining the impacts of environmental stressors on the different life stages of Nassau grouper.

Adult Nassau groupers are mesopredators (trophic level = 4.1; Froese & Pauly 2014) and play a vital role in maintaining the balance of coral reef ecosystems (Eggleston et al. 1998, Huntsman et al. 1999, Mumby et al. 2006, Stallings 2008, Mumby et al. 2012). They also form symbiotic relationships with cleaner species (e.g. Gobidae and Labridae) and are often observed at coral reef cleaning stations (Sluka et al. 1993, Sadovy & Eklund 1999). It has been estimated, using a combination of bioenergetic and experimental models, that aggregating groupers contribute significantly to nutrient supply, at 1.54 to 4.61 g m⁻² and 0.75 to 2.27 g m⁻² of nitrogen and phosphorus, respectively (Archer et al. 2015). Nassau grouper, therefore, play fundamental roles not only in trophic dynamics (as predators and prey) but also in wider aspects of ecosystem function and reef resilience.

REPRODUCTIVE BIOLOGY

Reproductive strategies of fish vary widely and have evolved to optimally provide for their offspring while balancing the ecophysiological costs to the

adults (Murua & Saborido-Rey 2003, Molloy et al. 2012). The reproductive potential of a species is dependent on several factors, including age and size at maturation (which generally correlate positively with gamete quality and fecundity), sex ratios, size and condition of breeding adults, as well as the timing and length of spawning events (Carter et al. 1991, Beldade et al. 2012, Choat 2012, Espigares et al. 2015).

The reproductive biology of Nassau grouper has been well studied (Shapiro 1987, Sadovy & Colin 1995, Watanabe et al. 1995b, Cushion et al. 2008, and references therein) due to its economic importance and the interest in the species for aquaculture. Nassau grouper are gonochoristic and reach sexual maturity between the ages of 4 and 8 yr (≥ 480 mm total length [TL]) (Sadovy & Colin 1995, Sadovy & Eklund 1999, Cushion et al. 2008, Froese & Pauly 2014). The species goes through a hermaphroditic stage as juveniles and adults are capable of sex change, although the drivers for sex change are not well established (Colin 1992, Watanabe et al. 1995a, Cushion et al. 2008). Sadovy & Colin (1995) identified environmental and social triggers as possible sex change drivers, but there has been no consensus on this and sex change in wild populations has not been documented.

Potential techniques for sex determination in wild fish populations that are not sexually dimorphic include the use of invasive (e.g. gonad removal; Cushion et al. 2008) and non-invasive (e.g. ultrasound; Whiteman et al. 2005) sampling techniques. Applying histology to determine gender and stage of sexual maturity requires terminal sampling, although techniques such as laparoscopy have also been employed to collect a small section of the gonad for staging from live fish (e.g. Falahatkar et al. 2011, Matsche et al. 2011). In some other fish species, DNA sex probes have been developed that can be applied non-destructively using a small fin clip or scale sample, e.g. for medaka (Matsuda et al. 1998), stickleback (Shikano et al. 2011), roach (Tyler & Jobling 2008) and salmon (Eisbrenner et al. 2014), but such a probe has not been developed for any grouper species. Development and utilisation of this technique for groupers seems to be logical given that fin clip samples are routinely collected for genetic analysis (Colin 2012). Additionally, analysis of previously collected fin clip samples could be compared with contemporary samples to report on any shifts in sex ratios that may have occurred and better understand the impacts of overexploitation on demographics and reproductive success.

Another approach to sex fish involves the measurement of blood vitellogenin—a precursor of egg yolk produced in female oviparous fish in response to oestrogens. Blood vitellogenin has been used as a non-destructive biomarker to effectively discriminate between males and females, even as juveniles, and to stage female ovary development. Heppell & Sullivan (1999) developed and successfully applied a vitellogenin-based enzyme-linked immunosorbent assay (VTG ELISA) to classify phases of sexual development in the grouper, *Mycteroperca microlepis*. The antibody for this assay has been shown to cross-react well with Nassau grouper VTG, allowing for its application to this species. Concentrations of VTG in blood plasma of female Nassau grouper have been measured at concentrations ranging between 0.02 and 4.66 mg ml⁻¹ and are positively correlated with sexually maturity (Heppell & Sullivan 1999). Measurement of VTG in wild fish has the potential to better establish demographics (e.g. spawning stock biomass and sex ratios), variability in spawning seasonality and viability of remaining spawning aggregations, but has yet to be applied in this regard.

Very little has been established relating to the function of sex steroid hormones in the reproductive cycle of Nassau grouper. Nassau grouper, however, have been successfully induced to spawn in laboratory settings using various steroid hormones, including carp pituitary hormone, luteinizing hormone-releasing hormone and human chorionic gonadotropin (Tucker & Woodard 1991, Watanabe et al. 1995a). Captive fish have also been observed spawning in aquaria and aquaculture cages without the use of hormone injections (Watanabe et al. 1995a, Tucker 1999). Reproduction in wild populations is thought to be density dependent (Colin 1992, Sala et al. 2001, Aguilar-Perera 2006), but the minimum threshold required to sustain a spawning aggregation has not been determined. Colin (1992) observed spawning in an aggregation containing as few as 10 Nassau grouper, but noted that overall spawning behaviour was reduced when compared with larger aggregations observed at other spawning sites during that period. This suggests that heavily fished spawning aggregation sites may have a lower relative productivity for any given fish biomass and are thus more susceptible to collapse than at less-exploited sites. Preferably, non-lethal sampling approaches should be used to assess the reproductive status and demographics of endangered Nassau grouper.

Nassau grouper migrate up to 300 km to and from their resident reefs along the continental shelf to reproduce at spawning sites (Bolden 2000, C. P.

Dahlgren et al. unpubl.). Migrating speeds and distances vary intraspecifically (Colin 1992, Bolden 2000, Starr et al. 2007, C. P. Dahlgren et al. unpubl.) and recent studies indicate that courtship-associated sounds play an integral role in facilitating this process. These auditory signals may also help first-time spawners to navigate to spawning sites (Schärer et al. 2012, Rowell et al. 2015). Analysis of movement patterns of tagged groupers suggest that females exhibit spawning site fidelity, often migrating past several spawning aggregations to reach their 'home' spawning site (Heppell et al. 2009, C. P. Dahlgren et al. unpubl.). In the Cayman Islands and Belize, 50% or more individuals make multiple spawning migrations (Semmens et al. 2007, Starr et al. 2007), but in The Bahamas fish appear to generally make single migrations (C. P. Dahlgren et al. unpubl., K. L. Stump et al. unpubl.).

Available information on spawning sites has shown they are highly diverse, varying in size, habitat type and water depth, but are often in close proximity to drop-offs and continental shelf edges (Smith 1972, Colin 1992; Aguilar-Perera & Aguilar-Dávila 1996, Whaylen et al. 2004, Heyman & Kjerfve 2008, Kobara & Heyman 2008, Kobara et al. 2013). The behavioural and physiological triggers associated with the formation and structure of migrating groups to, from and within spawning sites and the timing of gamete release remain poorly understood.

Migration and spawning activities have been linked to abiotic factors, including lunar phase, water temperature, tides and currents (Colin 1992, Shenker et al. 1993, Takemura et al. 2010, Heppell et al. 2011). Colin (1992) suggested that the optimal spawning temperature for Nassau grouper is between 25 and 26°C, which may explain latitudinal variation observed in the timing of spawning events throughout the species' geographic range. Reproduction in Nassau grouper is highly synchronised with the full moon (Sadovy & Eklund 1999). In other fish species that use lunar phases in the timing of their spawning, expressions of clock genes (e.g. *rfPer2*) have been shown to change with moonlight intensity and may be instrumental in regulating reproductive cycles (Takemura et al. 2010). However, no studies have examined the functional role of clock genes or other regulatory genes associated with the timing of reproduction in Nassau grouper. Such data would offer additional insights into the molecular mechanisms driving reproduction and help to explain observed differences in spawning seasonality of the species.

Reproduction via spawning aggregations may optimise fertilisation success, maximise larval survivor-

ship, and increase genetic mixing (Colin 1992, Domeier 2012). Patterns of larval dispersal, behaviour and retention throughout the native range of Nassau grouper have not been extensively investigated (Colin 1992, 1995, Heppell et al. 2009). Larval development occurs over a 35 to 50 d period, with a mean larval dispersal duration of 42 d (Tucker & Woodard 1991, Colin et al. 1997), followed by recruitment to macroalgal habitats as juveniles (25–35 mm TL) and a transition to reef habitats after 10 to 12 mo (Dahlgren & Eggleston 2001). Larval behaviour is not well understood and recruitment events are highly variable (Grover 1993, Shenker et al. 1993, Colin 1995, Colin et al. 1997, Grover et al. 1998, Heppell et al. 2011). Colin (1995) demonstrated that mesoscale gyres in the Exuma Sound could passively transport Nassau grouper recruits to natal spawning sites. Similar studies tracking the direction of surface and subsurface currents off the Little Cayman spawning aggregation site have shown that eddies retain larval Nassau grouper near spawning areas, which the authors postulate as a mechanism for self-recruitment (Heppell et al. 2011).

Various models have been developed to identify patterns of larval distribution. They include biophysical models such as the Lagrangian stochastic model, a larval tracking model of the Connectivity Modelling System (Paris et al. 2013) and the random-walk model (Rivera et al. 2011). With appropriate ecological (e.g. tagging studies; C. P. Dahlgren et al. unpubl.) and genetic data (e.g. parentage analysis; Almany et al. 2013), these models might usefully be applied to Nassau grouper to elucidate connectivity, source–sink dynamics and recruitment variability over broad spatial scales. Better understanding of survivorship in early life stages of Nassau grouper would provide key insights into larval distribution pathways and recruitment stochasticity, which would in turn clarify patterns of population structure and connectivity in adult fish. Addressing knowledge gaps in relation to the underlying mechanisms that influence and/or control the reproductive development and biology of Nassau grouper throughout its complete life history are required to set sustainable fishery targets and inform conservation management.

CONSERVATION STATUS AND SOCIOECONOMICS

Conservation status

Given its declining status, the Nassau grouper is now classified as Endangered on the IUCN Red List

(IUCN 2015) and threatened under the United States Endangered Species Act (Cornish & Eklund 2003, Albins et al. 2009). A variety of management measures have been implemented in an attempt to counteract the observed declines of Nassau grouper and to conserve the remaining populations in The Bahamas and throughout the Caribbean. Examples include size limits, partial or full seasonal closures, quotas, fishing bans, establishment of marine protected areas (MPAs) and FSA closures and FSA MPAs. The successes of these management strategies vary. For example, even after a complete moratorium on fishing for over 15 yr, the Nassau grouper fishery in Florida and Bermuda has still not recovered (Sadovy & Eklund 1999, Luckhurst 2001). In contrast, permanent fishing bans on Nassau grouper FSAs in the Cayman Islands and St. Thomas have been effective in assisting some of those populations to stabilise and recover from overfishing (Whaylen et al. 2004, 2007, Kadison et al. 2010, Heppell et al. 2012).

Nassau grouper fisheries management in The Bahamas

In the late 1980s, the Government of The Bahamas established a minimum 3 lb size limit (≥ 1.36 kg) for landed grouper and in 1998 a partial seasonal closure for Nassau grouper was imposed at the High Cay, Andros spawning aggregation site (under the Fisheries Resources (Jurisdiction and Conservation) Act CH.244-11, Part V; <http://laws.bahamas.gov.bs/cms/en>). The 3 lb size limit (≥ 480 mm TL) was based on size at first maturation data of Nassau grouper from the Caribbean (Sadovy & Eklund 1999). Because the resources required to consistently enforce all reported Nassau grouper FSAs in The Bahamas are inadequate, seasonal closures were implemented to prohibit the capture, sale and possession of Nassau grouper. As a consequence, all Nassau grouper are off-limits to fishing during part of the reproductive season. However, national seasonal closures to protect fish at other spawning sites were not established until 2004 (Table 1). The declaration of the closed season was left to the discretion of the Minister of Agriculture and Fisheries and this resulted in confusion and inconsistencies for many years (Table 1). During this period, the seasonal closure typically extended for 1 to 2 mo between December and February. Subsequent research has shown seasonal variation in Nassau grouper spawning, and they can reproduce earlier during the November full moon

Table 1. Management timeline for the Nassau grouper *Epinephelus striatus* fishery in The Bahamas

Year(s)	Management measure	Details
1958	Establishment of the first Marine Protected Area	Limitations placed on catching marine resources (including Nassau grouper) within the 456 km ² Exuma Cays Land and Sea Park
1986	Exuma Cays Land and Sea Park designated as a no-take marine reserve	All marine resources within the park's boundaries are protected
1987–1988	Fisheries Act sets minimum size limit	Landed grouper must be ≥3 lb (≥1.36 kg)
1998–1999	First partial closure of known Nassau grouper spawning aggregation site	High Cay, Andros is closed during the November–February full moons
2000	Partial closures of additional Nassau grouper spawning aggregation sites	Known spawning aggregation sites in Long Island are closed to fishing during the December full moon
2004	First national seasonal closure for Nassau grouper	Nassau grouper fishing banned during December–February
2005–2014	National seasonal closures	Annual closures set by the Minister of Agriculture and Fisheries. The closed season during this period varied from 1 to 3 mo
2015	Permanent annual seasonal closure established	Fisheries Act amended to prohibit fishing Nassau grouper during the months of December–February, which coincide with peak reproduction in The Bahamas

(Cushion et al. 2008, C. P. Dahlgren et al. unpubl.), suggesting that the current seasonal closure is insufficient. In 2015, the Fisheries Act was amended to include an annual 3 mo seasonal closure of Nassau grouper during 1 December–28 February. Additionally, all species within the boundaries of no-take marine reserves, e.g. the Exuma Cays Land and Sea Park (ECLSP), are protected from extraction activities including fishing. Despite seasonal closures and size restrictions, fishery-dependent data show steady declines in Nassau grouper landings throughout The Bahamas (Fig. 2).

Commercial fisheries landings

Commercial fishery landings data for The Bahamas is collected by the Department of Marine Resources (DMR). Historically, most Nassau grouper were landed in The Bahamas during the spawning season (Gascoigne 2002). Prior to 1994, Nassau grouper data were combined with data from all other grouper species, so figures on commercial landings for individual grouper species are only available for the period between 1994 and 2014. During this 20-yr period, a total of 4716 tonnes (t) of Nassau grouper were landed in The Bahamas, averaging 236 t yr⁻¹ (Fig. 2). Landings in The Bahamas declined to 70 t in 2012 from a peak of 514 t in 1997, with an overall decline of 86% over the past 2 decades (i.e. between

1994–2014) (Fig. 2). The DMR has acknowledged that commercial landings data in The Bahamas is often under-reported (see Cheung et al. 2013). Declines in Nassau grouper landings began before the implementation of the 2004 seasonal closure and have persisted for 20 yr. During the months of December–February, approximately 50 and 20% of Nassau grouper have been landed in The Bahamas

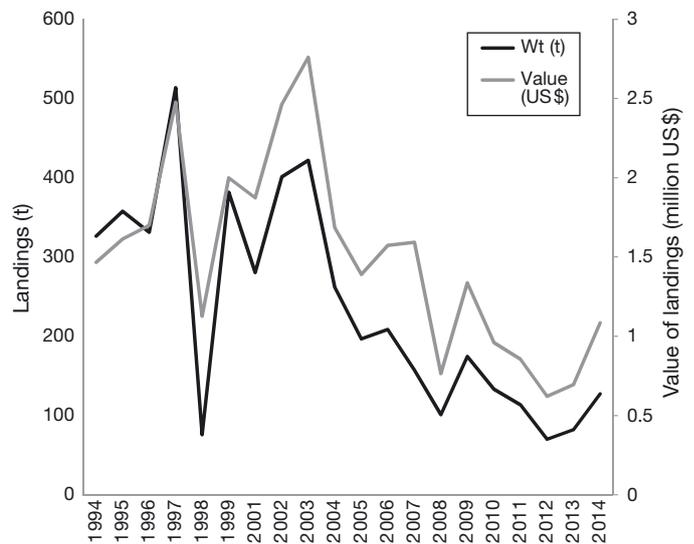


Fig. 2. Total commercial Nassau grouper *Epinephelus striatus* landings (weight and value) for The Bahamas during 1994–2014 as reported to The Bahamas Department of Marine Resources

before and after the implementation of the closed season. If the entire reproductive season (November–March) for the species is examined, 61 and 41% of fish have been landed in the country before and after seasonal closures. Available catch per unit effort (CPUE) data indicate declines over time (see Cheung et al. 2013). While the observed declines in CPUE may be due to a shift to other targeted species, the overall trend, coupled with the 20 yr decline in landings and the proportion of fish still harvested during the closed season, provides strong evidence to support that the Nassau grouper fishery is in serious decline. This is of major concern for The Bahamas, given that annual economic contributions from the fishery range between US\$ 620 thousand and 2.8 million, with an average of US\$1.5 million yr^{-1} (Fig. 2). It is also important to mention that these figures provide conservative estimates of the total fishery landings (see Cheung et al. 2013) and exclude revenue from recreational and tourism-related activities (Rudd & Tupper 2002). Economic valuation studies for Nassau grouper are needed (Rudd & Tupper 2002) and would be useful to help explain the socioeconomic benefits of conserving Nassau grouper to a broad range of stakeholders.

POPULATION STRUCTURE AND DYNAMICS

The Bahamas contains the largest proportion of global Nassau grouper spawning aggregation sites, with up to 30 located throughout the archipelago (Sadovy & Eklund 1999, Cheung et al. 2013, Kobara et al. 2013; Fig. 1). FSA research has been inconsistent and has focused on only a few sites from 3 islands: Bimini (Smith 1972, Gascoigne 2002), Andros (Ray 2000, Ehrhardt & Deleveaux 2007) and Long Island (Colin 1992). In contrast, consistent monitoring has been conducted at Nassau grouper FSAs in the Cayman Islands over a period of 10 yr (e.g. Whaylen et al. 2007) and in Puerto Rico for 11 yr (e.g. Schärer et al. 2010, Schärer-Umpierre et al. 2014). Vo et al. (2014) recently completed a stock assessment in the Turks and Caicos Islands where there are no management measures for Nassau grouper and have indicated that the population is relatively healthy (biomass of 0.58 t km^{-2} in 2008) compared with other parts of the Caribbean.

Attempts to evaluate the status of the Bahamian Nassau grouper fishery have relied heavily on fishery landings data, anecdotal information from fishers and modelling (Gascoigne 2002, Ehrhardt & Deleveaux 2007, Cheung et al. 2013). As an example, a

previous estimate on Nassau grouper stocks by Ehrhardt & Deleveaux (2007) was based on a single historical spawning aggregation site off High Cay, Andros. Their findings lacked *in situ* population data and were based on fishery landings and hydroacoustic assessments of fish abundances. Furthermore, the hydroacoustic assessments were not validated and there was a wide discrepancy in these data compared with diver observations of Nassau grouper at that site during the same period (Ray 2000). Divers reported abundances of fish at High Cay to be only 4 to 5% of hydroacoustic assessments (Ray 2000). The most recent studies from The Bahamas indicate abundances of Nassau grouper have declined over the past 2 decades between 70 and 90% in several historical locations (e.g. High Cay), and only 2 of 6 documented spawning aggregation sites in Long Island are still active (C. P. Dahlgren et al. unpubl. data). Visual observations estimate fish abundance at extant Long Island sites to be between only 200 and 700 grouper, far less than the thousands of fish reported in the past at these spawning aggregations (Colin 1992), although Colin (1992) did report that some of the FSAs in Long Island were fished out over the course of 1 to 2 spawning seasons. Similar observations of the rapid decline in abundance of Nassau grouper FSAs have also been reported from the Caribbean (e.g. Sala et al. 2001, Aguilar-Perera 2006). At present, the remaining stocks in The Bahamas experience high rates of poaching from local fishers, with up to 25 to 35% of fish removed from spawning aggregation sites annually (C. P. Dahlgren et al. unpubl. data). In contrast with other countries that have fewer spawning sites (e.g. Heyman & Requeña 2002, Heppell et al. 2012), very few reported Bahamian spawning aggregations have been validated through scientific methods (e.g. *in situ* diver surveys, telemetry, hydroacoustic assessments). Indeed, whether or not many of these locations still support active aggregations is essentially unknown. This is due in part to the logistical difficulties and financial costs associated with conducting fieldwork, especially in the remote areas where spawning sites often occur, and the lack of local capacity to collect data from widely dispersed spawning aggregation sites throughout the Bahamian archipelago. Population genetic approaches offer the potential to better establish population structure and dynamics over such an expansive area ($\sim 233\,000 \text{ km}^2$ of sea) and the fin clips or tissue samples required for these approaches could be collected with relative ease from live or recently killed specimens.

Overfishing is commonly cited as the primary cause for local collapses and global population

declines of Nassau grouper (Colin 1996, Aguilar-Perera 2006, Sadovy de Mitcheson et al. 2008, Albins et al. 2009, Cheung et al. 2013). Typically, larger individual groupers are removed from the population before they reproduce, which means that stocks are not being replenished. Removing the majority of large, highly fecund groupers over time is likely to reduce reproductive success and impact further on population sustainability (Heppell & Sullivan 1999, Sadovy & Domeier 2005) via decreasing genetic variability and thus population adaptability.

The use of molecular techniques to investigate genetic diversity, population structure and connectivity in marine ecosystems has increased substantially over the last 2 decades (Shulman & Bermingham 1995, Palumbi 2004, Cowen et al. 2006, Craig & Hastings 2007, Harrison et al. 2012, Beldade et al. 2014, Jackson et al. 2015). Molecular methods are now being applied in the assessments of population structure and genetic diversity (Silva-Oliveira et al. 2008), investigating evolutionary processes and local adaptation to natural or anthropogenic stressors (Paris et al. 2015), exploring genes controlling or regulating diseases (Teng et al. 2008), understanding sexual development (Luo et al. 2010), informing conservation management plans (Reiss et al. 2009) and in predicting the impacts of climate change (Nielsen et al. 2009, Davey et al. 2011, Horreo et al. 2011, Narum et al. 2013, Hemmer-Hansen et al. 2014). However, use of these approaches to understand the breeding biology and population dynamics of groupers is still in its infancy. Population structure in marine fish is influenced by interacting biological, ecological, environmental and anthropogenic processes and vary over spatial and temporal scales (see reviews by Nielsen et al. 2009, Reiss et al. 2009, Takemura et al. 2010, Hemmer-Hansen et al. 2014). Barriers to gene flow appear to be more subtle in the ocean, where larvae are dispersed with ocean currents and fish can migrate over vast distances (Lindeman et al. 2000, Palumbi 2004). This makes it challenging to assess population structure, dynamics and genetic differentiation in marine fish.

Polymorphic markers, such as DNA microsatellites or simple sequence repeats (SSR) and single nucleotide polymorphisms (SNPs), are now commonly used to more accurately assess genetic population structure and diversity among wild fish populations (Sunucks 2000, Hutchinson et al. 2001, Zatzoff et al. 2004, Hauser & Carvalho 2008, Griffiths et al. 2010, Hohenlohe et al. 2010, Wang et al. 2013, Paris et al. 2015). Although evidence of population structuring has been documented in coral reef fish (e.g. Shulman

& Bermingham 1995, Bay et al. 2008), only a few studies have assessed population structure in Epinephelinae groupers (Rivera et al. 2004, 2011, Zatzoff et al. 2004, Maggio et al. 2006, Silva-Oliveira et al. 2008, Beldade et al. 2014, Jackson et al. 2014, 2015) and there is a paucity of information regarding genotypic variation within and among spawning aggregations generally.

Using polymorphic DNA microsatellite loci, Zatzoff et al. (2004) found populations of red grouper *E. morio*, the most closely related species to Nassau grouper, and scamp *Mycteroperca phenax*, another aggregating marine fish, to be genetically similar. Both species are heavily fished, but no discernable effects on genetic diversity and population structure were detected from samples across the Atlantic and Gulf of Mexico (Zatzoff et al. 2004). Silva-Oliveira et al. (2008) also found no evidence of subpopulation structure in goliath grouper *E. itajara* from Brazil. In contrast, restriction fragment length polymorphism of NADH dehydrogenase (ND2) revealed that Atlantic and Mediterranean dusky grouper *E. marginatus* populations were genetically distinct (Maggio et al. 2006). Cytochrome sequence analysis provided further evidence for genetic variation and a growing population within the Mediterranean (Maggio et al. 2006). Similarly, Rivera et al. (2011) also found distinct populations of Hawaiian grouper *E. quernus*. Comparisons of microsatellite and mitochondrial DNA (mtDNA) data with pelagic larval dispersal models were used to demonstrate high connectivity between Hawaiian grouper populations and to identify important source-sink areas. This information was used to recommend protection of Hawaiian groupers in the mid-archipelago, an area where the highest levels of genetic diversity were observed (Rivera et al. 2011). Jackson et al. (2015) used a similar approach for leopard grouper *M. rosacea* in the Gulf of California to inform marine reserve design that would protect areas with the greatest genetic diversity and support connectivity between subpopulations.

Information on the genetic population structure and dynamics of Nassau grouper populations is scarce (Hateley 1995, Stevenson et al. 1998, Jackson et al. 2014; Table 2). Earlier assessments on Nassau grouper populations using enzyme electrophoresis and mtDNA showed low to moderate genetic variation, suggesting the existence of a single population comprised of randomly mating individuals in the northern Caribbean (Hateley 1995). Given that statistical measures used in population genetics (e.g. heterozygosity and F_{ST}) are based on frequencies of

Table 2. Chronological summary of available genetic data on Nassau grouper. The number of microsatellite loci used in each study is reported in square brackets

Year	Location (no. of sites)	No. of DNA samples	Techniques used	Purpose	Source
1998	Belize (4) USA (1) Cuba (1) The Bahamas (1)	396 97 21 23	Microsatellites [2]	Population structure	Stevenson et al. (1998)
2005	Cayman Islands (2) Turks and Caicos (1) Belize (1) The Bahamas (1)	Total: 264	Protein electrophoresis [20]	Population structure	Hateley (1995)
2012	Belize (1) Cayman Islands (1) US Virgin Islands (1)	50 50 50	Microsatellites [10]	Microsatellite primer development	Abelló et al. (2012) and Jackson et al. (2012)
2012	Cayman Islands (2) US Virgin Islands (1)	20 20	Microsatellites [15]	Microsatellite primer development	Bernard et al. (2012)
2014	Mexico (1) Belize (4) Cuba (2) Cayman Islands (3) USA (1) The Bahamas (3) Turks and Caicos (1) Puerto Rico (1) US Virgin Islands (1) British Virgin Islands (1) Antigua (1)	Total: 620	Mitochondrial DNA, microsatellites [9] and single nucleotide polymorphisms	Population structure	Jackson et al. (2014)

alleles, highly polymorphic microsatellite loci spread throughout the genome considerably increase the resolution and replication required to differentiate between populations when compared with maternally inherited mtDNA (see reviews by Sunnucks 2000 and Selkoe & Toonen 2006). More recently, Jackson et al. (2014) used a suite of molecular markers, including microsatellites, mtDNA and SNPs, to investigate genetic connectivity and variability of Nassau grouper populations throughout the Caribbean and The Bahamas. They found considerable regional variation in the genetic composition of Nassau grouper with evidence of subpopulations and suggested that these differences may be attributed to oceanographic variability, which restricts larval dispersal (Jackson et al. 2014).

Spawning migrations observed through the tagging of Nassau grouper in the central Bahamas are an order of magnitude greater in distance compared with other parts of the Caribbean region (C. P. Dahlgren et al. unpubl.) and appear to be consistent with genetic evidence of population structure in The Bahamas. Differences in the elemental composition of otoliths from fish from The Bahamas and Belize also provide evidence in support of regional and

within-country population substructuring (Patterson et al. 1999). Bahamian populations of Nassau grouper may be self-sustaining and genetically distinct compared with other populations (Patterson et al. 1999, Cowen et al. 2006, Jackson et al. 2014). Yet, the genetic diversity, structure and effective population sizes (N_e) of Nassau grouper populations remain poorly understood and unquantified for most of The Bahamas. Currently, microsatellites and SNPs appear to provide the best resolution for understanding the genetic architecture and current demographics of these fish and detecting whether any recent changes have occurred to their population structure (Jackson et al. 2014).

Previous research has shown that reduced genetic diversity and variation in wild fish populations is often linked to drastic declines in effective population size, which can occur because of overfishing or historical bottlenecks (Smith et al. 1991). Understanding whether Nassau grouper populations in The Bahamas are comprised of single or multiple populations as well as the intraspecific differences and current demographics (i.e. abundance, age, sex ratios and size) of remaining populations is key to developing a robust conservation management strategy for

the fishery. Although Nassau grouper aquaculture may be promising, it is unclear how successful restocking initiatives would be without knowledge of genetic diversity and population structure of wild stocks (Roberts et al. 1995, Benetti 2014), which have adapted to survive and reproduce under environmental conditions that vary spatially.

Future research should be directed to expand knowledge regarding spatiotemporal patterns of genetic connectivity, population structure, differentiation, larval dispersal and recruitment using high-resolution genome-wide molecular markers, such as microsatellites and SNPs. These assessments will be greatly improved by using recently developed species-specific microsatellite primers for Nassau grouper (Bernard et al. 2012, Jackson et al. 2012) that have already been used in population genetic studies in parts of the Caribbean (e.g. Jackson et al. 2014).

ADDRESSING FUTURE RESEARCH NEEDS

The efficacy of various management measures for conserving the species is under evaluation (C. P. Dahlgren et al. unpubl. data), but fishery-dependent and independent data suggest inadequacies in the current approaches. For example, the size limit of fish landed needs to be amended from ≥ 3 lb (≥ 1.36 kg) to ≥ 5 lb (≥ 2.27 kg) to ensure that the species is allowed to reproduce at least once prior to capture. Although Nassau grouper may attain sexual maturity from ~ 3 lb (≥ 480 mm TL), first time migrators in The Bahamas are 540 mm TL or greater (C. P. Dahlgren et al. unpubl.). This differs from observations in the Caribbean, where size at first migration is ≥ 440 mm TL (e.g. Semmens et al. 2007). An improved data collection system is needed to more accurately capture landings data for the country to include sizes of fish, capture sites, dates, etc. Such information is important to understand national trends in abundance, size distribution of harvested specimens and CPUE.

Of the threats known to negatively impact Nassau grouper, overfishing—most notably at aggregation areas—is particularly detrimental. Failure to stem the decline in populations of Nassau grouper in The Bahamas is likely due to a number of factors including: (1) high market demand and non-compliance with established fishery regulations; (2) inadequate enforcement; and (3) limited understanding of reproductive biology, population structure and dynamics to inform fishery regulations. While increased funding may help to tackle issues relating to the capacity to enforce regulations and increase education and

outreach efforts, from an ecological or biological perspective, the following questions need to be addressed to assist with improving conservation management for the species:

- (1) How genetically diverse and connected are Nassau grouper populations within The Bahamas?
- (2) What are the demographics, spawning stock sizes and predominant migration patterns of remaining Nassau grouper FSAs?
- (3) What are the impacts of overfishing on the reproductive potential or success of the species?
- (4) How should future no-take MPAs be designed to account for genetic connectivity and promote population recovery?

Spawning seasonality and migration patterns

Smith (1972) hypothesized that Nassau grouper migrate along continental shelf edges to FSAs. External tagging for mark-recapture studies and acoustic telemetry (e.g. Bolden 2000, Sala et al. 2001, Semmens et al. 2007, Starr et al. 2007), which involves the surgical implantation of acoustic tags to track fish movement, has proven useful in elucidating spatiotemporal patterns of Nassau grouper migrations. Investigations of Nassau grouper migratory behaviour have shown intraspecific differences with respect to movements both within home ranges (0.1–0.2 km) and along migratory pathways during the spawning season, where fish travel distances of 25 to >300 km (Carter et al. 1991, Colin 1992, Bolden 2000, Aguilar-Perera 2006, Semmens et al. 2007, Starr et al. 2007, Stevens-McGeever et al. 2013, C. P. Dahlgren et al. unpubl., K. L. Stump et al. unpubl.). However, in The Bahamas, migratory corridors, demographics (i.e. sex composition, size and age structure) of aggregating fish, and their origins remain largely unknown, and evidence suggests that they may be different from other parts of the Caribbean, and even within the country (C. P. Dahlgren et al. unpubl., K. L. Stump et al. unpubl.). Tagging and acoustic telemetry can be used to determine the origins of aggregators, reveal potential locations of FSAs, migratory pathways, migration frequency, FSA site fidelity, and connectivity between home reefs and Nassau grouper FSAs over various spatial scales (e.g. Bolden 2000, Semmens et al. 2007, Starr et al. 2007, Heppell et al. 2009, C. P. Dahlgren et al. unpubl., K. L. Stump et al. unpubl.). This type of information is critical to understand patterns of connectivity, inform marine spatial planning and prioritize enforcement efforts for active FSAs.

Genetic diversity and population connectivity

An important component of biodiversity conservation is genetic diversity (Moritz 2002). Yet, the extent to which gene flow is exchanged and migratory pathways occur among Nassau grouper FSAs and home reefs, in addition to source–sink dynamics of the species throughout the country's protected area system, is unknown. This is because little attention has been paid to migration patterns of adult fish species and the links between larval connectivity and genetic population structuring in the spatial design of existing MPAs in The Bahamas. Instead MPAs have been established based on opportunism and basic principles of marine reserve design, and socioeconomic, cultural and political considerations (Ray 1998, Moultrie 2012). Some Bahamian MPAs were created to conserve ecologically and economically valuable species and diverse marine habitats and to replenish important fishery species (e.g. Nassau grouper) through spillover effects (Sluka et al. 1996, Brumbaugh 2014). Indeed, several of the habitats required by Nassau grouper, including nearshore areas and deeper coral reef systems, are protected within parts of The Bahamas National Protected Area System (BNPAS).

For example, the oldest of the country's MPAs, the ECLSP, has some of the highest densities of Nassau grouper in The Bahamas and in the Caribbean region (Sluka et al. 1996, 1997, Dahlgren 2004, Stallings 2009, Dahlgren et al. 2016). This 456 km² no-take marine reserve encompasses both terrestrial and marine habitats, including seagrasses, mangroves, hard bottom areas, patch, fringing and forereefs (Sherman et al. 2013), supporting diverse fish and benthic communities. However, studies by Bolden (2000) and C. P. Dahlgren et al. (unpubl.) show that Nassau grouper migrate outside the ECLSP to spawn. These findings underscore the critical importance of integrating knowledge of reproductive biology and population dynamics into marine spatial planning. More recently, principles of MPA design have been refined to integrate connectivity at ecologically relevant scales (Botsford et al. 2009, White 2015). The Bahamas is working towards incorporating genetic structure and population connectivity into its MPA network for Caribbean spiny lobster *Panulirus argus*, staghorn coral *Acropora cervicornis*, elkhorn coral *Acropora palmata* and Nassau grouper through coupled biophysical larval dispersal models and genetic analysis (Kough et al. 2013, C. Paris pers. comm., K. D. Sherman et al. unpubl. data).

The Bahamas has entered into an agreement to implement the Program of Work on Protected Areas and, as part of the United Nations Convention on Biological Diversity and Caribbean Challenge Initiative, declared to protect 20% of its nearshore marine habitats by 2020 (Moultrie 2012). The designation of future MPAs that are to become a part of the BNPAS should not only be based on core principles of marine reserve design, but also take into account genetic diversity, population structure and connectivity, along with socioeconomic and cultural considerations. This type of MPA network would likely increase ecological and socioeconomic benefits to the country's populace and promote ecosystem resiliency.

Monitoring and stock assessments of FSAs

Available data suggest that spawning aggregations evolved to provide a suite of biological and ecological advantages to promote the survival of both adults and offspring by optimizing reproductive success and mediating interacting effects of predators and prey (Nielsen et al. 2009, Choat 2012, Domeier 2012, Molloy et al. 2012). However, very few studies have tested this and the evolutionary mechanisms associated with spawning aggregations remain unclear (Choat 2012), representing an important area for future research. Consistent monitoring of the status of Nassau grouper in home reefs and nearshore nursery habitats should be conducted to investigate trends or habitat-associated shifts in abundance and size distribution. Similarly, continued monitoring of Nassau grouper FSAs is also required to understand temporal variability in spawning behaviour and dynamics, and document recovery and/or declines of spawning stock biomass. Traditional ecological monitoring during the spawning and non-spawning periods will provide a better understanding of the health and population structure of Nassau grouper, which is fundamental to creating appropriate stock-recruitment management models. Such a model does not exist for The Bahamas and its development will help to ensure that sustainable exploitation rates are set to maintain a healthy fishery and the livelihoods of local fishers.

ADDRESSING BARRIERS TO IMPLEMENTATION

Although precautionary approaches (e.g. marine reserves) have been implemented to conserve Nassau grouper, these strategies have not necessarily

been effective at preventing further fishery declines (Fig. 2; Cheung et al. 2013, K. D. Sherman et al. unpubl. data). Marine protected area design, therefore, needs to include all aspects of a species' life history as well as spatial and temporal variability in population structure and dynamics, habitat connectivity, and spawning migration corridors, for optimal effectiveness (Chiappone et al. 2000, Grüss et al. 2014, Pittman et al. 2014, Rowell et al. 2015, C. P. Dahlgren et al. unpubl.).

The socioeconomic gaps that need to be addressed to improve compliance for fishery regulations are beyond the scope of this review. However, research has shown that recognising and assessing stakeholder perspectives is an important aspect of this process (Hilborn et al. 2005, Robinson et al. 2014, Wilson et al. 2016). These types of analyses are necessary to capture local knowledge, incentivise support, address misconceptions and change attitudes regarding the Nassau grouper fishery. Co-management approaches (e.g. Hilborn et al. 2005) should be integrated into management strategies to strengthen compliance for fisheries regulations and to reduce costs associated with enforcement. A combined approach, integrating tagging studies with genetic analysis, stock assessment modelling and FSA monitoring would yield insights into ecologically significant migratory corridors, reproductively successful and genetically diverse and/or distinct FSAs, and population structure of Nassau groupers throughout the archipelago. This information could be used to reveal areas where increased enforcement is warranted or new management measures need to be implemented. In doing so, the maximum benefits can be reaped from the limited resources available for monitoring and enforcement. Therefore, we strongly recommend a holistic approach that combines population genetics, acoustic telemetry, biophysical modelling and *in situ* ecological monitoring to provide a more rigorous and adaptive framework, to better inform conservation management strategies. This would vastly improve our understanding and lead to strengthened protection for remaining endangered Nassau grouper populations.

Acknowledgements. Mr Lindy Knowles, Science Officer for the Bahamas National Trust created the map of Nassau grouper FSAs. The Bahamas fishery data were provided to K.D.S by Michael Braynen and Lester Gittens of the Department of Marine Resources (Nassau, Bahamas). Financial support was provided to K.D.S. from the Shirley Oakes Butler (Overseas) and (Bahamian) Charitable Trust via the Lyford Cay Foundation and the East Nassau Rotary Club Foundation and to C.P.D. by the Atlantis Blue Project Foun-

dation and a grant to the Perry Institute for Marine Science by the Disney Conservation Fund's Reverse The Decline Program. We have no conflicts of interest to declare. Constructive criticism of 4 anonymous reviewers greatly improved the manuscript.

LITERATURE CITED

- Abelló P, Ai WM, Altmann C, Bernardi G and others (2012) Permanent genetic resources added to Molecular Ecology Resources Database 1 April 2012–31 May 2012. *Mol Ecol Resour* 12:972–974
- Aguilar-Perera A (2006) Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast. *Mar Ecol Prog Ser* 327:289–296
- Aguilar-Perera A, Aguilar-Dávila W (1996) A spawning aggregation of Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environ Biol Fishes* 45:351–361
- Albins MA, Hixon MA, Sadovy Y (2009) Threatened fishes of the world: *Epinephelus striatus* (Bloch, 1792) (Serranidae). *Environ Biol Fishes* 86:309–310
- Almany GR, Hamilton RJ, Bode M, Matawai M and others (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Curr Biol* 23:626–630
- Archer SK, Heppell SA, Semmens BX, Pattengill-Semmens CV, Bush PG, McCoy CM, Johnson BC (2012) Patterns of color phase indicate spawn timing at a Nassau grouper *Epinephelus striatus* spawning aggregation. *Curr Zool* 58:73–83
- Archer SK, Allgeier JE, Semmens BX, Heppell SA and others (2015) Hot moments in spawning aggregations: implications for ecosystem-scale nutrient cycling. *Coral Reefs* 34:19–23
- Baldwin CC, Johnson GD (1993) Phylogeny of the Epinephelinae (Teleostei: Serranidae). *Bull Mar Sci* 52:240–283
- Bay LK, Caley MJ, Crozier RH (2008) Meta-population structure in a coral reef fish demonstrated by genetic data on patterns of migration, extinction and re-colonisation. *BMC Evol Biol* 8:248
- Beets J, Hixon MA (1994) Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. *Bull Mar Sci* 55:470–483
- Beldade R, Holbrook SJ, Schmitt RJ, Planes S, Malone D, Bernardi G (2012) Larger female fish contribute disproportionately more to self-replenishment. *Proc R Soc B* 279:2116–2121
- Beldade R, Jackson AM, Cudney-Bueno R, Raimondi PT, Bernardi G (2014) Genetic structure among spawning aggregations of the gulf coney *Hyporhamphus acanthistius*. *Mar Ecol Prog Ser* 499:193–201
- Benetti D (2014) New venture in Bahamas focuses on grouper, other high-value marine fish. *Global Aquaculture Advocate* Nov/Dec 2014:42–44
- Bernard AM, Feldheim KA, Richards VP, Nemeth RS, Shivji MS (2012) Development and characterization of fifteen novel microsatellite loci for the Nassau grouper (*Epinephelus striatus*) and their utility for cross-amplification on a suite of closely related species. *Conserv Genet Resour* 4:983–986
- Bolden SK (2000) Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fish Bull* 98:642–645

- Botsford LW, Brumbaugh DR, Grimes C, Kellner JB and others (2009) Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Rev Fish Biol Fish* 19:69–95
- Brumbaugh DR (2014) Guide to the science of marine protected areas in The Bahamas. American Museum of Natural History, New York, NY
- Buchan KC (2000) The Bahamas. *Mar Pollut Bull* 41:94–111
- Camp EF, Lohr KE, Barry SC, Bush PG, Jacoby SA, Manfrino C (2013) Microhabitat associations of late juvenile Nassau Grouper (*Epinephelus striatus*) off Little Cayman. *Bull Mar Sci* 89:571–581
- Carter J, Marrow GJ, Pryor V (1991) Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proc Gulf Caribb Fish Inst* 43:65–111
- Cheung WWL, Sarmiento JL, Dunne J, Frölicher TL and others (2012) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat Clim Change* 3:254–258
- Cheung WWL, Sadovy de Mitcheson Y, Braynen MT, Gittens LG (2013) Are the last remaining Nassau grouper *Epinephelus striatus* fisheries sustainable? Status quo in the Bahamas. *Endang Species Res* 20:27–39
- Chiappone M, Sluka R, Sullivan Sealey K (2000) Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Mar Ecol Prog Ser* 198:261–272
- Choat JH (2012) Spawning aggregations in reef fishes: ecological and evolutionary processes. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Springer, New York, NY, p 85–116
- Coleman FC, Koenig CC, Collins A (1996) Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fish spawning aggregations. *Environ Biol Fishes* 47:129–141
- Coleman FC, Koenig CC, Huntsman GR, Musick JA and others (2000) Long-lived reef fishes: the grouper-snapper complex. *Fisheries* (Bethesda, Md) 25:14–21
- Coleman FC, Koenig CC, Scanlon KM, Heppell S, Heppell S, Miller MW (2010) Benthic habitat modification through excavation by red grouper, *Epinephelus morio*, in the northeastern Gulf of Mexico. *The Open Fish Sci J* 3:1–15
- Colin PL (1992) Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environ Biol Fishes* 34:357–377
- Colin PL (1995) Surface currents in Exuma Sound, Bahamas and adjacent areas with reference to potential larval transport. *Bull Mar Sci* 56:48–57
- Colin PL (1996) Longevity of some coral reef fish spawning aggregations. *Copeia* 1996:189–192
- Colin PL (2012) Timing and location of aggregation and spawning in reef fishes. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Springer, New York, NY, p 117–158
- Colin PL, Laroche WA, Brothers EB (1997) Ingress and settlement in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. *Bull Mar Sci* 60:656–667
- Cornish A, Eklund AM (2003) *Epinephelus striatus*. The IUCN red list of threatened species, Version 2014.2. www.iucnredlist.org (accessed on 23 October 2014)
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522–527
- Craig MT, Hastings PA (2007) A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini. *Ichthyol Res* 54:1–17
- Craig MT, Heemstra PC, Sadovy YJ (2011) Groupers of the world: a field and market guide. National Inquiry Services Centre (NISC), Grahamstown
- Cushion N, Sullivan-Sealey K (2008) Landings, effort and socio-economics of a small scale commercial fishery in The Bahamas. *Proc Gulf Caribb Fish Inst* 600:162–166
- Cushion N, Cook M, Schull J, Sullivan-Sealey K (2008) Reproductive classification and spawning seasonality of *Epinephelus striatus* (Nassau grouper), *E. guttatus* (red hind) and *Mycteroperca venenosa* (yellowfin grouper) from The Bahamas. *Proc 11th Int Coral Reef Symp, Ft Lauderdale, Florida* 22:994–998
- Dahlgren C (2004) Bahamian marine reserve: past experience and future plans. In: Sobel J, Dahlgren C (eds) Marine reserves: a guide to science, design and use. Island Press, Washington, DC, p 268–286
- Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227–2240
- Dahlgren CP, Eggleston DB (2001) Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. *Mar Ecol Prog Ser* 217:145–156
- Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM and others (2006) Marine nurseries and effective juvenile habitats: concepts and applications. *Mar Ecol Prog Ser* 312:291–295
- Dahlgren C, Sherman K, Lang J, Kramer PR, Marks K (2016) Bahamas coral reef report card. Vol. 1: 2011–2013. Nassau, Bahamas, www.nature.org/media/bahamas/bahamas-coral-reef-report-card.pdf
- Davey JW, Hohenlohe PA, Etter PD, Boone JQ, Catchen JM, Blaxter ML (2011) Genome-wide genetic marker discovery and genotyping using next-generation sequencing. *Nat Rev Genet* 12:499–510
- Domeier ML (2012) Revisiting spawning aggregations: definitions and challenges. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Springer, New York, NY, p 1–20
- Eggleston DB (1995) Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. *Mar Ecol Prog Ser* 124:9–22
- Eggleston DB, Grover JJ, Lipcius RN (1998) Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. *Bull Mar Sci* 63:111–126
- Ehrhardt NM, Deleveaux VKW (2007) The Bahamas' Nassau grouper (*Epinephelus striatus*) fishery—two assessment methods applied to a data-deficient coastal population. *Fish Res* 87:17–27
- Eisbrenner WD, Botwright N, Cook M, Davidson EA and others (2014) Evidence for multiple sex-determining loci in Tasmanian Atlantic salmon (*Salmo salar*). *Heredity* 113:86–92
- Ellis SC, Watanabe WO, Ellis EP (1997) Temperature effects on feed utilization and growth of postsettlement stage Nassau grouper. *Trans Am Fish Soc* 126:309–315

- Espigares F, Rocha A, Molés G, Gómez A, Carrillo M, Zanuy S (2015) New insights into the factors mediating the onset of puberty in sea bass. *Gen Comp Endocrinol* 224: 176–185
- Falahatkar B, Tolouei G, Mohammad H, Falahatkar S, Abbasalizadeh A (2011) Laparoscopy, a minimally-invasive technique for sex identification in cultured great sturgeon *Huso huso*. *Aquaculture* 321:273–279
- FAO (Food and Agriculture Organization) (2014) The state of world fisheries and aquaculture opportunities and challenges 2014. FAO, Rome
- Froese R, Pauly D (eds) (2014) FishBase. www.fishbase.org (accessed on 23 October 2014)
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Gascoigne J (2002) Nassau grouper and queen conch in The Bahamas: status and management options. MacAlister Elliot and Partners, Lymington, p 1–44, <https://brief.org/wp-content/uploads/2015/03/BREEF-NGrouperQConchStatusReport2002.pdf>
- Griffiths AM, Machado-Schiaffino G, Dillane E, Coughlan J and others (2010) Genetic stock identification of Atlantic salmon (*Salmo salar*) populations in the southern part of the European range. *BMC Genet* 11:31
- Grover JJ (1993) Trophic ecology of pelagic early-juvenile Nassau grouper, *Epinephelus striatus*, during an early phase of recruitment into demersal habitats. *Bull Mar Sci* 53:1117–1125
- Grover JJ, Eggleston DB, Shenker JM (1998) Transition from pelagic to demersal phase in early-juvenile Nassau grouper, *Epinephelus striatus*: pigmentation, squamation and ontogeny of diet. *Bull Mar Sci* 62:97–113
- Grüss A, Robinson J, Heppell SS, Heppell SA, Semmens BX (2014) Conservation and fisheries effects of spawning aggregation marine protected areas: What we know, where we should go, and what we need to get there. *ICES J Mar Sci* 71:1515–1534
- Harikrishnan R, Balasundaram C, Heo MS (2011) Fish health aspects in grouper aquaculture. *Aquaculture* 320: 1–21
- Harrison HB, Williamson DH, Evans RD, Almany GR and others (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr Biol* 22: 1023–1028
- Hateley JG (1995) Preliminary results of a protein electrophoretic analysis of genetic variation, population structure and gene flow in the Nassau grouper, *Epinephelus striatus*. *Proc Gulf Caribb Fish Inst* 47:888–905
- Hauser L, Carvalho GR (2008) Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. *Fish Fish* 9:333–362
- Heemstra PC, Randall JE (1993) FAO species catalogue, Vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae): an annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper, and lyretail species known to date. FAO Fisheries Synopsis No. 125, Food and Agriculture Organization of the United Nations, Rome
- Hemmer-Hansen J, Overgaard TN, Pujolar JM (2014) Population genomics of marine fishes: next-generation prospects and challenges. *Biol Bull* 227:117–132
- Heppell SA, Sullivan CV (1999) Gag (*Mycteroperca microlepis*) vitellogenin: purification, characterization and use for enzyme-linked immunosorbent assay (ELISA) of female maturity in three species of grouper. *Fish Physiol Biochem* 20:361–374
- Heppell SA, Semmens BX, Pattengill-Semmens CV, Bush PG and others (2009) Tracking potential larval dispersal patterns from Nassau grouper aggregation sites: evidence for local retention and the ‘importance of place’. *Proc Gulf Caribb Fish Inst* 61:325–327
- Heppell SA, Semmens BX, Pattengill-Semmens CV, Bush PG and others (2011) Oceanographic patterns associated with Nassau grouper aggregation spawn timing: shifts in surface currents on the nights of peak spawning. *Proc Gulf Caribb Fish Inst* 63:152–154
- Heppell SA, Semmens BX, Archer SK, Pattengill-Semmens CV and others (2012) Documenting recovery of a spawning aggregation through size frequency analysis from underwater laser callipers measurements. *Biol Conserv* 155:119–127
- Heyman WD, Kjerfve B (2008) Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bull Mar Sci* 83:531–551
- Heyman W, Requeña N (2002) Status of multi-species spawning aggregations in Belize. The Nature Conservancy, Punta Gorda
- Hilborn R, Orensanz JM, Parma AM (2005) Institutions, incentives and the future of fisheries. *Phil Trans R Soc B Biol Sci* 360:47–57
- Hohenlohe PA, Bassham S, Etter PD, Stiffler N, Johnson EA, Cresko WA (2010) Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. *PLoS Genet* 6:e1000862
- Horreo JL, Machado-Schiaffino G, Ayllon F, Griffiths AM, Bright D, Stevens JR, Garcia-Vazquez E (2011) Impact of climate change and human-mediated introgression on southern European Atlantic salmon populations. *Glob Change Biol* 17:1778–1787
- Huntsman GR, Potts J, Mays RW, Vaughan D (1999) Groupers (Serranidae, Epinephelinae): endangered apex predators of reef communities. In: Musick JA (ed) *Life in the slow lane: ecology and conservation of long-lived marine animals*. *Am Fish Soc Symp* 23:217–231
- Hutchinson WF, Carvalho GR, Roger SI (2001) Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. *Mar Ecol Prog Ser* 223:251–260
- IUCN (International Union for Conservation of Nature) (2015) IUCN red list of threatened species, Version 2015-3. www.iucnredlist.org (accessed on 03 July 2015)
- Jackson AM, Semmens BX, Bernardi G (2012) Characterization and cross-species amplification of microsatellite markers in Nassau grouper (*Epinephelus striatus*). *Mol Ecol Resour* 12:972–974
- Jackson AM, Semmens BX, Sadovy de Mitcheson Y, Nemeth RS and others (2014) Population structure and phylogeography in Nassau grouper (*Epinephelus striatus*), a mass-aggregating marine fish. *PLoS One* 9:e97508
- Jackson AM, Munguía-Vega A, Beldade R, Erisman BE, Bernardi G (2015) Incorporating historical and ecological genetic data for leopard grouper (*Mycteroperca rosacea*) into marine reserve design in the Gulf of California. *Conserv Genet* 16:811–822
- Kadison E, Nemeth RS, Blondeau J, Smith T, Calnan J (2010) Nassau Grouper (*Epinephelus striatus*) in St. Thomas, US Virgin Islands, with evidence for a spawning aggregation site recovery. *Proc Gulf Caribb Fish Inst* 62:273–279

- Kobara S, Heyman WD (2008) Geomorphometric patterns of Nassau grouper (*Epinephelus striatus*) spawning aggregation sites in the Cayman Islands. *Mar Geod* 31: 231–245
- Kobara S, Heyman WD, Pittman SJ, Nemeth RS (2013) Biogeography of transient fish spawning aggregations in the Caribbean: a synthesis for future research and management. *Oceanogr Mar Biol Annu Rev* 51:281–326
- Kough AS, Paris CB, Butler MJIV (2013) Larval connectivity and the international management of fisheries. *PLoS One* 8:e64970
- Lindeman KC, Pugliese R, Waugh GT, Ault JS (2000) Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bull Mar Sci* 66:929–956
- Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809
- Luckhurst BE (2001) Policies, legislation and management options: workshop report 'working towards sustainable management of Nassau groupers in Belize'. Belize City, 30 July, 2001. Green Reef Environmental Institute, Belize City
- Luo YS, Hu W, Liu XC, Lin HR, Zhu ZY (2010) Molecular cloning and mRNA expression pattern of *Sox9* during sex reversal in orange-spotted grouper (*Epinephelus coioides*). *Aquaculture* 306:322–328
- Maggio T, Andaloro F, Arculeo M (2006) Genetic population structure of *Epinephelus marginatus* (Pisces, Serranidae) revealed by two molecular markers. *Ital J Zool* 73: 275–283
- Matsche MA, Bakal RS, Rosemary KM (2011) Use of laparoscopy to determine sex and reproductive status of shortnose sturgeon (*Acipenser brevirostrum*) and Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*). *J Appl Ichthyology* 27:627–636
- Matsuda M, Matsuda C, Hamaguchi S, Sakaizumi M (1998) Identification of the sex chromosomes of the medaka, *Oryzias latipes*, by fluorescence *in situ* hybridization. *Cytogenet Cell Genet* 82:257–262
- Molloy PP, Côté IM, Reynolds JD (2012) Why spawn in aggregations? In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management, Springer, New York, NY, p 57–84
- Moritz C (2002) Strategies to protect biological diversity and the evolutionary processes that sustain it. *Syst Biol* 51: 238–254
- Morris A, Roberts C, Hawkins J (2000) The threatened status of groupers (Epinephelinae). *Biodivers Conserv* 9: 919–942
- Moultrie S (2012) Master plan for The Bahamas national protected area system. The Nature Conservancy, Northern Caribbean Office, Nassau
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV and others (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- Mumby PJ, Steneck RS, Edwards AJ, Ferrari R, Coleman R, Harborne AR, Gibson JP (2012) Fishing down a Caribbean food web relaxes trophic cascades. *Mar Ecol Prog Ser* 445:13–24
- Muñoz RC, Currin CA, Whitfield PE (2011) Diet of invasive lionfish on hard bottom reefs of the Southeast USA: insights from stomach contents and stable isotopes. *Mar Ecol Prog Ser* 432:181–193
- Murua H, Saborido-Rey F (2003) Female reproductive strategies of marine fish species of the North Atlantic. *J Northwest Atl Fish Sci* 33:23–31
- Musick JA (1999) Criteria to define extinction risk in marine fishes: the American Fisheries Society Initiative. *Fisheries* (Bethesda, Md) 24:6–14
- Narum SR, Buerkle CA, Davey JW, Miller MR, Hohenlohe PA (2013) Genotyping-by-sequencing in ecological and conservation genomics. *Mol Ecol* 22:2841–2847
- Nielsen EE, Hemmer-Hansen J, Larsen PF, Bekkevold D (2009) Population genomics of marine fishes: identifying adaptive variation in space and time. *Mol Ecol* 18: 3128–3150
- Palumbi SR (2004) Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annu Rev Environ Resour* 29:31–68
- Paris CB, Helgers J, van Sebille E, Srinivasan A (2013) Connectivity modelling system: a probabilistic modelling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environ Model Softw* 42:47–54
- Paris JR, King RA, Stevens JR (2015) Human mining activity across the ages determines the genetic structure of modern brown trout (*Salmo trutta* L.) populations. *Evol Appl* 8:573–585
- Patterson HM, Thorrold SR, Shenker JM (1999) Analysis of otolith chemistry in Nassau grouper (*Epinephelus striatus*) from The Bahamas and Belize using solution-based ICP-MS. *Coral Reefs* 18:171–178
- Pittman SJ, Monaco ME, Friedlander AM, Legare B and others (2014) Fish with chips: tracking reef fish movements to evaluate size and connectivity of Caribbean marine protected areas. *PLoS One* 9:e96028
- Ray C (1998) Bahamian protected areas part 1: how it all began. *Bahamas J Sci* 6:2–10
- Ray GC (2000) Investigations of Nassau grouper breeding aggregations at High Cay, Andros: implications for a conservation strategy. Final Report, Department of Fisheries, Nassau
- Reiss H, Hoarau G, Dickey-Collas M, Wolff WJ (2009) Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish Fish* 10:361–395
- Rivera MAJ, Kelley CD, Roderick GK (2004) Subtle population genetic structure in the Hawaiian grouper, *Epinephelus quernus* (Serranidae) as revealed by mitochondrial DNA analyses. *Biol J Linn Soc* 81:449–468
- Rivera MAJ, Andrews KR, Kobayashi DR, Wren JLK, Kelley C, Roderick GK, Toonen RJ (2011) Genetic analyses and simulations of larval dispersal reveal distinct populations and directional connectivity across the range of the Hawaiian Grouper (*Epinephelus quernus*). *J Mar Biol* 2011:1–11
- Roberts CM, Quinn N, Tucker JW, Woodward PN (1995) Introduction of hatchery-reared Nassau grouper to a coral reef environment. *N Am J Fish Manage* 15:159–164
- Robinson J, Samoilys MA (2013) Reef fish spawning aggregations in the Western Indian Ocean: research for management. WIOMSA Book Series 13. WIOMSA, CORDIO, Nairobi
- Robinson J, Cinner JE, Graham NA (2014) The influence of fisher knowledge on the susceptibility of reef fish aggregations to fishing. *PLoS One* 9:e91296
- Rowell TJ, Nemeth RS, Schärer MT, Appeldoorn RS (2015) Fish sound production and acoustic telemetry reveal behaviors and spatial patterns associated with spawning aggregations of two Caribbean groupers. *Mar Ecol Prog*

- Ser 518:239–254
- Rudd MA, Tupper MH (2002) The impact of Nassau grouper size and abundance on scuba diver site selection and MPA economics. *Coast Manage* 30:133–151
- Russell MW, Sadovy de Mitcheson Y, Erisman BE, Hamilton RJ, Luckhurst BE, Nemeth RS (2014) Status report: world's fish aggregations 2014. Science and Conservation of Fish Aggregations, California, USA. International Coral Reef Initiative
- Sadovy Y, Colin PL (1995) Sexual development and sexuality in the Nassau grouper. *J Fish Biol* 46:961–976
- Sadovy Y, Domeier M (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs* 24:254–262
- Sadovy Y, Eklund AM (1999) Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792) and the Jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Tech Rep NMFS 146
- Sadovy de Mitcheson Y, Colin PL (eds) (2012) Reef fish spawning aggregations: biology, research and management, Vol. 35: fish and fisheries. Springer, New York, NY
- Sadovy de Mitcheson YS, Erisman B (2012) Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Springer, New York, NY, p 225–284
- Sadovy de Mitcheson Y, Cornish A, Domeier M, Colin PL, Russell M, Lindeman KC (2008) A global baseline for spawning aggregations of reef fishes. *Conserv Biol* 22:1233–1244
- Sadovy de Mitcheson Y, Craig MT, Bertocini AA, Carpenter KE and others (2013) Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish Fish* 14:119–136
- Sala E, Ballesteros E, Starr RM (2001) Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* (Bethesda, Md) 26:23–30
- Schärer MT, Nemeth MI, Appeldoorn RS (2010) Protecting a multi-species spawning aggregation at Mona Island, Puerto Rico. *Proc Gulf Caribb Fish Inst* 62:252–259
- Schärer MT, Rowell TJ, Nemeth MI, Appeldoorn RS (2012) Sound production associated with reproductive behavior of Nassau grouper *Epinephelus striatus* at spawning aggregations. *Endang Species Res* 19:29–38
- Schärer-Umpierre M, Nemeth R, Tuohy E, Clouse K, Nemeth M, Appeldoorn RS (2014) Nassau grouper *Epinephelus striatus* fish spawning aggregations in the US Caribbean. *Proc Gulf Caribb Fish Inst* 66:408–412
- Schoelinc C, Hinsinger D, Dettai A, Cruaud C, Justine JL (2014) A phylogenetic re-analysis of groupers with applications for ciguatera fish poisoning. *PLoS One* 9:e98198
- Selkoe KA, Toonen RJ (2006) Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecol Lett* 9:615–629
- Semmens BX, Luke KE, Bush PG, Pattengill-Semmens C, Johnson B, McCoy C, Heppell S (2007) Investigating the reproductive migration and spatial ecology of Nassau grouper (*Epinephelus striatus*) on Little Cayman Island using acoustic tags — an overview. *Proc Gulf Caribb Fish Inst* 58:199–206
- Semmens BX, Bush P, Heppell S, Johnson B, McCoy C, Pattengill-Semmens C, Whaylen L (2008) Charting a course for Nassau grouper recovery in the Caribbean: what we've learned and what we still need to know. *Proc Gulf Caribb Fish Inst* 60:607–609
- Shapiro DY (1987) Reproduction in groupers. In: Polvina JJ, Ralston SR (eds) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, CO, p 295–327
- Shenker JM, Maddox ED, Wishinski E, Pearl A, Thorrold SR, Smith N (1993) Onshore transport of settlement-stage Nassau grouper *Epinephelus striatus* and other fishes in Exuma Sound, Bahamas. *Mar Ecol Prog Ser* 98:31–43
- Sherman KD, Dahlgren CP, Brumbaugh DR, Knowles LC (2013) Tourism and coral reef health in the Exuma Cays Land and Sea Park. *Proc Gulf Caribb Fish Inst* 65:234–242
- Shikano T, Herczeg G, Merilä J (2011) Molecular sexing and population genetic inference using a sex-linked microsatellite marker in the nine-spined stickleback (*Pungitius pungitius*). *BMC Res Notes* 4:119
- Shulman MJ, Bermingham E (1995) Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution* 49:897–910
- Silva-Oliveira GC, do Rêgo PS, Schneider H, Sampaio I, Vallinoto M (2008) Genetic characterisation of populations of the critically endangered Goliath grouper (*Epinephelus itajara*, Serranidae) from the Northern Brazilian coast through analyses of mtDNA. *Genet Mol Biol* 31:988–994
- Sluka R, Chiappone M, Sullivan KM, Garine-Wichatitsky D (1993) Benthic habitat characterization and space utilization by juvenile epinepheline groupers in the Exuma Cays Land and Sea Park, Central Bahamas. *Proc Gulf Caribb Fish Inst* 45:23–36
- Sluka R, Chiappone M, Sullivan KM, Wright R (1996) Habitat and life in the Exuma Cays, The Bahamas: the status of groupers and coral reefs in the Northern Cays. Media Publishing, Nassau
- Sluka R, Chiappone M, Sullivan KM, Wright R (1997) The benefits of a marine fishery reserve for Nassau Grouper *Epinephelus striatus* in the Central Bahamas. *Proc 8th Int Coral Reef Symp* 2:1961–1964
- Smith CL (1972) A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). *Trans Am Fish Soc* 101:257–261
- Smith PJ, Francis RICC, McVeagh M (1991) Loss of genetic diversity due to fishing pressure. *Fish Res* 10:309–316
- Stallings CD (2008) Effects of an exploited predator on recruitment of coral-reef fishes. *Ecology* 89:2090–2095
- Stallings CD (2009) Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. *PLoS One* 4:e5333
- Starr RM, Sala E, Ballesteros E, Zabala M (2007) Spatial dynamics of the Nassau grouper *Epinephelus striatus* in a Caribbean atoll. *Mar Ecol Prog Ser* 343:239–249
- Stevens-McGeever SJ, Semmens BX, Pattengill-Semmens C, Heppell S, Bush P, Johnson B, McCoy C (2013) Alterations in home range space over a multi-year study of Nassau grouper (*Epinephelus striatus*). *Proc Gulf Caribb Fish Inst* 65:204
- Stevenson DE, Champman RW, Sedberry GR (1998) Stock identification in Nassau grouper, *Epinephelus striatus*, using microsatellite DNA analysis. *Proc Gulf Caribb Fish Inst* 50:727–749
- Sunday JM, Calosi P, Dupont S, Munday PL, Stillman JH, Reusch TBH (2014) Evolution in an acidifying ocean. *Trends Ecol Evol* 29:117–125

- Sunnucks P (2000) Efficient genetic markers for population biology. *Trends Ecol Evol* 15:199–203
- Takemura A, Rahman MS, Park YJ (2010) External and internal controls of lunar-related reproductive rhythms in fishes. *J Fish Biol* 76:7–26
- Teng Y, Hou Z, Gong J, Liu H and others (2008) Whole-genome transcriptional profiles of a novel marine fish iridovirus, Singapore grouper iridovirus (SGIV) in virus-infected grouper spleen cell cultures and in orange-spotted grouper, *Epinephelus coioides*. *Virology* 377: 39–48
- Tucker JW Jr (1999) Grouper aquaculture. Southern Regional Aquaculture Center Publication No. 721, Stoneville, MS
- Tucker JW Jr, Woodard PC (1991) Growth and development of domestic juvenile Nassau groupers. *Proc Gulf Caribb Fish Inst* 43:389–391
- Tyler CR, Jobling S (2008) Roach, sex, and gender-bending chemicals: the feminization of wild fish in English rivers. *Bioscience* 58:1051–1059
- Vo AE, Ashley MC, Dikou A, Newman SP (2014) Fishery exploitation and stock assessment of the endangered Nassau Grouper, *Epinephelus striatus* (Actinopterygii: Perciformes: Serranidae) in the Turks and Caicos Islands. *Acta Ichthyol Piscat* 44:117–122
- Wang L, Liu S, Zhuang Z, Guo L, Meng Z, Lin H (2013) Population genetic studies revealed local adaptation in a high gene-flow marine fish, the small yellow croaker (*Larimichthys polyactis*). *PLoS One* 8:e83493
- Watanabe WO, Ellis SC, Ellis EP, Head WD and others (1995a) Progress in controlled breeding of Nassau grouper (*Epinephelus striatus*) broodstock by hormone induction. *Aquaculture* 138:205–219
- Watanabe WO, Lee CS, Ellis SC, Ellis EP (1995b) Hatchery study of the effects of temperature on eggs and yolk sac larvae of the Nassau grouper *Epinephelus striatus*. *Aquaculture* 136:141–147
- Watson AC, Siemann LA, Hanlon RT (2014) Dynamic camouflage by Nassau groupers *Epinephelus striatus* on a Caribbean coral reef. *J Fish Biol* 85:1634–1649
- Western Central Atlantic Fishery Commission (2014) The first meeting of the CFMC/WCAFC/OSPESCA/CRFM working group on spawning aggregations, Report No. 1059. FAO Fisheries and Aquaculture, Bridgetown
- Whaylen L, Pattengill-Semmens CV, Semmens BX, Bush PG, Boardman MR (2004) Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. *Environ Biol Fishes* 70: 305–313
- Whaylen L, Bush PG, Johnson BC, Luke KE and others (2007) Aggregation dynamics and lessons learned from five years of monitoring at a Nassau grouper (*Epinephelus striatus*) spawning aggregation in Little Cayman, Cayman Islands, BWI. *Proc Gulf Caribb Fish Inst* 59: 413–422
- White JW (2015) Marine reserve design theory for species with ontogenetic migration. *Biol Lett* 11:20140511
- Whiteman EA, Jennings CA, Nemeth RS (2005) Sex structure and potential female fecundity in a *Epinephelus guttatus* spawning aggregation: applying ultrasonic imaging. *J Fish Biol* 66:983–995
- Wilson RS, Hardisty DJ, Epanchin-Neill RS, Runge MC and others (2016) A typology of time-scale mismatches and behavioral interventions to diagnose and solve conservation problems. *Conserv Biol* 30:42–49
- Young JL, Bornik ZB, Marcotte ML, Charlie KN, Wagner GN, Hinch SG, Cooke SJ (2006) Integrating physiology and life history to improve fisheries management and conservation. *Fish Fish* 7:262–283
- Zatcoff MS, Ball AO, Sedberry GR (2004) Population genetic analysis of red grouper, *Epinephelus morio*, and scamp, *Mycteroperca phenax*, from the southeastern U.S. Atlantic and Gulf of Mexico. *Mar Biol* 144:769–777

Editorial responsibility: Inna Sokolova,
Charlotte, North Carolina, USA

Submitted: December 22, 2015; Accepted: May 11, 2016
Proofs received from author(s): July 5, 2016