



**On the dynamics of coral reef fishes:
Growth, senescence and mortality**

Submitted by **Shay O'Farrell** to the University of Exeter
as a thesis for the degree of
Doctor of Philosophy in Biological Sciences
in September **2011**

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Abstract

The present thesis deals with the related themes of mortality and growth in coral reef fishes. In the first chapter, a nine-year dataset from Bermuda is used to quantify how reef fish populations respond to the introduction of a trap-fishing ban, finding that herbivores exhibit extremely strong recovery, but that stock-recruitment relationships may be decoupled by a numerical response in a meso-predator. In the second chapter, a dataset from Bonaire is used to test the efficacy of the widely-used coefficient of natural mortality, M , in modelling a population of stoplight parrotfish (*Sparisoma viride*). As determined from simulation models, this statistical coefficient performs considerably less well than a novel mechanistic function that partitions mortality into size- and age-based processes and achieves extremely good fits to the field data. The third chapter presents a new approach to estimating growth parameters of reef fish from tagging data that exploits the disproportionate response of certain parameters to misestimates in the true age of the tagged individuals. The method works considerably better than the most widely used method when sample sizes are small, as is commonly the case in reef fish tagging studies where recapture rates tend to be low. The fourth and final chapter uses non-lethal stable isotope techniques to tease apart the invasion dynamics of Indo Pacific lionfish (*Pterois* spp.) that are currently colonising the wider Caribbean. The results show that lionfish exhibit habitat-specific ontogenetic shifts in prey selection, inflicting elevated mortality on small, bommie-dwelling fishes on forereefs but switching to seagrass-foraging invertivores as they grow. Lionfish also display ontogenetically shifting competition with native Nassau grouper (*Epinephelus striatus*), which may provide a greater barrier to invasion success on patch reefs than on fore reefs, where competitive overlap is diminished. The thesis concludes with a discussion of some lines of enquiry that could not be undertaken owing to time or data limitations, but which may hold as much interest for the reader as they do for the author.

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Declaration of Author Contributions

Chapter 1: *General Introduction*

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Chapter 2: *Density-dependent response of coral reef herbivores and meso predators to a fishery closure*

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Chapter 6: *General Discussion*

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1

General Introduction

Coral reef ecosystems are highly variable in space and time and, as the product of such environments, reef fish populations have evolved in a dynamic context. Consequentially, modelling the population dynamics of coral reef fishes presents numerous challenges in the estimation of vital rates such as growth and mortality, even in undisturbed populations. However, most fish populations in the wider Caribbean have undergone varying levels of perturbation, frequently underpinned by the introduction of novel mortality through fishing or the arrival of invasive species. The present thesis deals with some of these aspects of reef fish dynamics, ranging from approaches to estimating vital parameter values and incorporating them into biologically informed models, to the trophodynamic characterisation of an invasive predator.

Modelling populations of wildlife is essential for their management, as it allows the likely impacts of management actions to be explored. This is especially true of fishes, which are unusual in that they are often managed explicitly so they can continue to be exploited by extraction (fisheries), which no longer happens with most other wild populations. Modelling of mortality is thus especially important, as fisheries mortalities will act in addition to natural mortality. Historically, natural mortality in fishes tends to have been modelled as a single, time-invariant rate of population decay, often known as ‘background mortality’. However, this approach assumes that the probability of mortality is the same for all individuals regardless of traits such as age or size. That mortality should act in such a manner seems unlikely (Vetter, 1988) and one of the aims of the present work is to test this assumption in coral reef fishes, where numerous studies (e.g., Dahlgren and Eggleston 2000, Almany and Webster 2006, Craig et al. 2006) have shown that mortality varies during the life of a fish.

Although models are imperfect representations of the world, they allow researchers to understand how study systems behave and even to explore the probable consequences of changing circumstances. However, even the best-designed model can only be as good as the data on which it has been parameterised. In the study of fishes, obtaining accurate somatic growth parameters is challenging, and generally requires either the sacrifice of individuals in order to estimate age from hard body parts such as otoliths, or repeated capture and measurement of marked individuals. Both of these approaches require relatively large sample sizes ($n > 50$) to obtain accurate values, yet for many fish populations, sacrificing such a large number of individuals is not acceptable, but low

recapture rates would require the marking of many hundreds of individuals. In the present work, we develop a novel method for estimating the parameters of the most commonly used fish growth model, the von Bertalanffy growth function, from small numbers of recaptures.

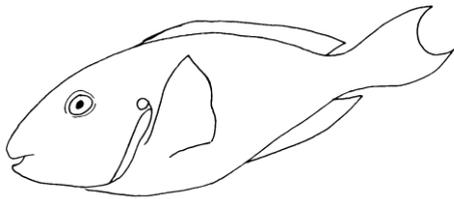
Even with biologically appropriate and accurately parameterised models, a challenge that commonly confronts fish researchers is teasing apart the community dynamics induced by a given management action. Because of the tightly interlinked fish communities on coral reefs, a change in the population of a given species may force changes in other species with which it interacts. Such interactions can even occur indirectly, making them even more difficult to elucidate. However, a management intervention imposed in Bermuda affords the rare opportunity to pull apart some interspecific dynamics that are commonly obscured. The Bermudan government banned the use of fish traps but permitted the continuation of hook-and-line fishing (Trott and Luckhurst 2007), amounting to a *de facto* ban on herbivore fishing with the continued fishing of predators. A comprehensive dataset of fish community structure permits the situation to be exploited and provides a glimpse into the internal dynamics of herbivore population recovery that is commonly obscured by the commensurate recovery of predator populations.

Not only can the fishing of native predators cause changes to community dynamics, but so too can the arrival of novel predators (Morris and Akins 2009). As predation is one of the fundamental processes structuring coral reef fish communities (Almany and Webster 2006), such events may force reorganisation of native community composition, within which there will likely be winners and losers. The invasion of the Caribbean by Indo Pacific lionfish, *Pterois* spp., heralded a period of changing community dynamics on the host reefs, although whether these changes will become permanent remains to be seen. A dataset of stable isotope measurements taken from organisms at multiple trophic levels affords insights to the impacts of the invasion on native competitors and prey items. With particular focus on the native Nassau grouper, *Epinephelus striatus*, the analysis presented here uses the lens of stable isotope ecology to peer into the obscurity of trophic interactions that may subtly yet profoundly alter the dynamics of an invaded community.

The reader will be familiar with many of the concepts covered in this thesis but may not be as familiar with the study organisms themselves. This section aims to provide an introduction to the organisms, in order to provide the reader with background biological information and to give context to why these species are of interest. Although many species are dealt with in the text, three will be covered here in detail as they represent three of the most important facets of the work: herbivory, predation and invasion. The herbivore presented is the Caribbean stoplight parrotfish,

Sparisoma viride, the predator is the Nassau grouper, *Epinephelus striatus*, and the invader is the complex of Indo Pacific lionfish species, *Pterois volitans/miles*, that has recently been introduced to the wider Atlantic region.

The herbivore: *Sparisoma viride*



The availability of hard substrate is one of the main limiting factors on coral reefs, where scleractinian corals must compete with macroalgae for space (Buddemeier et al. 2004). Modern coral reef communities have evolved such that herbivorous grazers facilitate the continuing

prevalence of corals, and a reduction in herbivory has been shown to increase macroalgal biomass, negatively impacting on the ability of corals to compete with the algae for space (Williams and Polunin 2001). To understand this relationship, it is useful to look back to its origins. Coral reefs have existed since the Ordovician (450 Ma) although their form has changed considerably in that time (Bellwood and Wainwright 2002). Modern scleractinian-dominated reefs and modern reef fish families appear and begin to diversify at around the same time in the fossil record when scleractinian corals and herbivores embarked on a mutualistic relationship that would shape coral reefs into their modern form (Bellwood and Wainwright 2002).

Mesozoic assemblages were typified by carnivorous fishes, and reef associations were probably indirect, perhaps providing shelter (Bellwood and Wainwright 2002). Grazing was predominantly undertaken by low-mobility non-excavating invertebrates. Around the start of the Cenozoic (65.5 Ma), however, deep-grazing limpets and urchins appear. Fish-based herbivory on coral reefs also traces its origin to the late Mesozoic/early Cenozoic when several herbivore groups appear, including epilithic algal grazers and algal browsers. These herbivores moved to reefs from other habitats and began dramatically to reshape Cenozoic reefs. For the first time, grazers were durophagous and highly mobile, combining intensive grazing with high selectivity. The herbivores facilitated coral dominance through cropping of algal competitors, and in turn received shelter from the myriad predators that continue to characterise reef fish communities into the Holocene (Bellwood and Wainwright 2002).

Until 1983, the Caribbean long-spined sea urchin, *Diadema antillarum*, was the most important macroalgal grazer on Holocene Caribbean coral reefs (but see Hughes 1994), and their populations

were capable of fluctuating in response to macroalgal abundance and of exerting tight controls on macroalgal growth (Levitan 1988)(but see Hughes 1994). When disease catastrophically reduced the *D. antillarum* population in 1983 (Lessios et al. 1984) the die-off resulted in substitution within the key grazing role, with parrotfishes (Actinopterygii | Perciformes | Scaridae) becoming the paramount grazers on most reefs (Mumby 2006, Mumby et al. 2006).

Work conducted by Mumby et al. (2006) in the Bahamas showed a strong negative relationship between macroalgal cover and parrotfish grazing intensity, the latter reducing macroalgal cover by a factor of four inside the Exuma Cays Land and Sea Park. However, since the occurrence of the urchin mass-mortality, macroalgal cover on Caribbean coral reefs has increased relative to scleractinian coral cover (Williams and Polunin 2001), and the role of scarids in controlling macroalgal cover can be considered to be increasingly critical in maintaining ecosystem integrity.

Scarids have a clear fossil history and are a derived clade of Labridae . The habitat association pattern evident in the scarid cladogram implies that the scarids were originally seagrass dwellers (15 Ma) before moving onto reefs only 5 Ma, and scarids' highly modified jaw and pharyngeal mill probably evolved for eating seagrasses and their epiphytes (Bellwood and Wainwright 2002).

One of the most interesting aspects of scarid biology is their sexual ontogeny. Within the Caribbean, fishes of the genus *Sparisoma* are necessarily born female, but those of the genus *Scarus* may be born as either sex (Choat and Robertson 1975). Only certain scarids exhibit specific juvenile phase colouration, but all species exhibit both initial- and terminal-phase colouration. Within the genus *Sparisoma*, fishes displaying initial phase colouration can be either male or female and can be sexually mature or immature, but terminal-phase colouration is exclusive to sexually mature males. Within the genus *Scarus*, however, sexually mature males never display initial colouration (Hawkins and Roberts 2003).

The stoplight parrotfish, *Sparisoma viride* (Bonnaterre) is a conspicuous member of western Atlantic coral reef fish communities from Brazil to Bermuda (Robins and Ray 1986, Cervigón et al. 1992) and is the scarid species on which the present work most focuses. *S. viride* has a particularly complex and fascinating life history. Active during daylight hours, it preferentially grazes on dead coral substrate (McAfee and Morgan 1996) covered in algal turfs and containing a high content of endolithic algae (Bruggemann et al. 1994) although it also eats particular macro-algae (Mumby 2006, Mumby et al. 2006, Mumby et al. 2007) and has been observed to bite living corals (Littler et al. 1989) and sponges (Dunlap and Pawlik 1996, Wulff 1997). Its benthic association, vivid

colouration and non-cryptic behaviour make *S. viride* an easy target for spear fishing and, although it has long been exploited in countries such as Jamaica and Dominica (Hawkins and Roberts 2003), in many other countries the species remains unfished. However, this situation may soon change as dwindling coral reef fish stocks throughout the region (Newton et al. 2007) force shifts in fisheries targets.

S. viride is a sexually dichromatic (Winn and Bardach 1957) sequential hermaphrodite with a complex and variable life history (vanRooij et al. 1996b, Hawkins and Roberts 2003). All species within the genus *Sparisoma* are protogynous and sex-change is not obligatory, with some fish remaining female regardless of how large they grow. This contrasts with members of other genera such as *Scarus* which will become male if they live long enough (Robertson and Warner 1978). At sites where there is a sufficiently-developed back reef area, populations of *S. viride* generally consist of four life phases, namely immature juveniles, females, territorial males and non-territorial ('bachelor') males, with the adult fish predominantly structured as two distinct yet interacting groups. One group restricts itself to the deeper region abutting the reef front and the other occupies the shallower back reef (Cardwell 1989, Koltés 1993, vanRooij et al. 1995).

The deep group is comprised of males that guard territories containing 'harems' of females consisting of up to 14 individuals (vanRooij et al. 1996c). Territorial males habitually chase conspecific males from their territories whilst ignoring the ingress of fishes that share their diet, supporting the hypothesis that territories are primarily maintained for mating purposes (vanRooij et al. 1996a). Similarly, intruding conspecific females are chased from territories by harem females, usually of comparable body size. In contrast, the shallow group fish do not maintain territories but rather form loose aggregations, and although they spend most of their time roving the back reef they also make regular forays to the reef front. Group fidelity is very high, and although there is a degree of migration from the shallows to the deep, the inverse is negligible (vanRooij et al. 1996c).

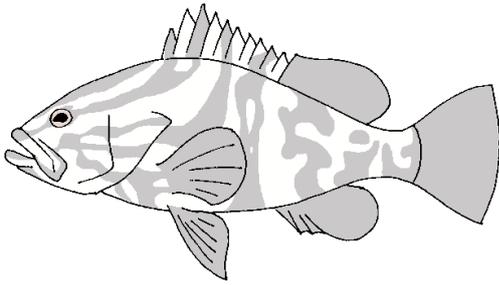
In the shallows there are no apparent barriers to entry and population density is far higher than in the deep with up to 80% of the adult population sharing as little as 23% of the reefal area (vanRooij et al. 1996c). Furthermore, the fact that shallow food resources are of lower yield than in the deep (vanRooij et al. 1996a) suggests that the shallow population is regulated by inter- and intra-specific competition for food, although it is of course possible that recruitment limitation may also play a role in regulating the populations (Doherty and Fowler, 1994). In the deep reef, by contrast, the limited reefal area and the vigour with which territories are guarded support the assumption that population density is limited by competition for space. *S. viride* reproduce through pair spawning,

when territorial males mate with multiple females from both the deep and shallow groups (vanRooij et al. 1996c). Spawning occurs in or near the deep water adjacent to the territories, and because *S. viride* reproduce daily on a year-round basis, proximity to the reef front confers a large advantage and it is assumed by the author that this is the preferred habitat for adults.

During spawning, each female and territorial male pair simultaneously release milt and eggs into the water column where fertilisation occurs and a planktonic larval phase begins, after which juveniles settle to the reef as females of around 1 cm length (vanRooij et al. 1996b). Distributing themselves throughout multiple habitats across the reef, they remain sexually immature until around 15-17 cm (vanRooij et al. 1996b). Maturation presents the possibility of changing sex which is, as for many reef fish, a strategic gamble between the immediate, but modest, reproductive success of a female and the delayed, but enhanced, success of a territorial male (Muñoz and Warner 2004).

If a mature fish remains female she may commence reproducing without delay but because she must spawn with one of the relatively scarce territorial males she will be forced into competition with the other females, thereby limiting her reproductive potential. Alternatively, a mature fish may change sex and join the shallow group as a bachelor male who does not spawn but invests available energy in growth on the chance that if he becomes large enough he may be able to win a territory when an incumbent territorial male dies (vanRooij et al. 1995). The elevated reproductive output that comes with territoriality subsequently compensates for the spawning foregone during the ‘bachelor years’ and the reward is very high for males that succeed: territorial males have been observed to mate on average six times a day, and up to a maximum of 13 times (vanRooij et al. 1996c).

The native predator: *Epinephelus striatus*



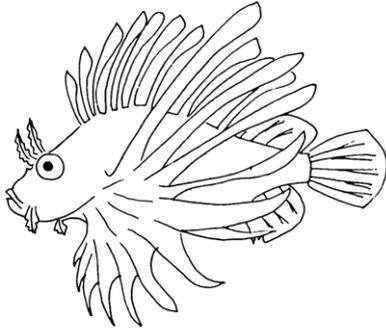
As with the parrotfishes, the groupers (Actinopterygii | Perciformes | Serranidae, subfamily: Epinephelinae) are protogynous hermaphrodites (Randall 1967). Although common in coral reef assemblages, they can also be found in deep water and in subtropical regions where true

reefs are absent, but they are invariably marine (Choat and Bellwood 1991). As is common in hermaphroditic fishes, their social system is complex, and groupers may engage in a wide range of reproductive strategies from pair-bonding to group spawning (Warner 1991). Although some members of the Serranidae family such as anthias (subfamily: Anthiinae) are planktivorous, all of the groupers are predatory.

The Nassau grouper, *Epinephelus striatus*, was one of the most widely distributed Serranids in the western Atlantic and was a major fisheries target for much of the twentieth century (Jory and Iverson 1989). A benthic-associated generalist predator, *E. striatus* is an important piscivore in Caribbean reef fish assemblages (Hixon and Beets 1993) which also feeds on crustaceans and molluscs (Albins et al. 2009) and is found on high relief coral reefs and rocky bottoms to depths of at least 130 m (Jory and Iverson 1989, Albins et al. 2009). Reaching a maximum length of over a metre and weight of 20 kg, *E. striatus* undergoes sex change from female to male at lengths between 300 and 800 mm and males may be expected to have spent at least one reproductive season as a female (Jory and Iverson 1989).

E. striatus historically were observed forming enormous aggregations at habitual spawning sites, with group size estimated at over 100,000 individuals (Smith 1972, Miller 1984). The resulting juveniles settle to macroalgal beds after which they may progress to patch reefs and finally to offshore reefs upon reaching adulthood (Eggleston 1995), the timing of the ontogenetic shift driven by a trade-off between the relative safety of the juvenile habitat against the elevated opportunity for growth presented by the adult habitat (Dahlgren and Eggleston 2000). Unfortunately, the tendency to spawn at specific times and locations has made *E. striatus* particularly vulnerable to overexploitation (Sadovy and Eklund 1999, Albins et al. 2009) leading to dramatic region-wide decline in abundance, and the once-common species is now listed as *endangered* on the IUCN Red List of Threatened Species (IUCN 2011).

The invader: *Pterois volitans/miles*



Perhaps the broadest division in reef fish phylogeography is that between the species of the Indo Pacific and the Atlantic, which may be traced back to the Terminal Tethyan Event (TTE) when a land bridge was raised between Africa and Eurasia sometime between 18 and 12 Ma, splitting tropical marine biota into two groups (Bellwood and Wainwright 2002). After aeons of separation, however, anthropogenic processes are starting to bring these diverged lineages back into contact, in few cases as spectacularly as the recent invasion of the western Atlantic by the Indo Pacific lionfish complex, *Pterois volitans/miles* (Actinopterygii | Scorpaeniformes | Scorpaenidae), hereafter *lionfish*.

Although there are anecdotal reports of lionfish sightings in the wider Caribbean going back to the 1980s (Morris and Whitfield 2009), the majority of individuals probably trace their origin to 1992 when Hurricane Andrew destroyed a number of seafront aquaria in Florida (Courtenay 1995, Whitfield et al. 2002). The lionfish has become established on both euphotic and mesophotic reefs throughout the tropical and sub-tropical western Atlantic, and is now the dominant species on some reefs (Green and Côté 2009). The rate at which the invader has achieved such success may be surprising given the low densities in which it occurs in its natural distribution, but there is precedence as *Pterois miles* successfully invaded the Mediterranean in the 1980s (Golani and Sonin 1992). However, the species is relatively unstudied in its home range, and the few papers that exist have mostly been published since the invasion (Morris and Whitfield 2009). What is known, however, is that they are voracious predators of fishes and invertebrates (Albins and Hixon 2008, Morris and Akins 2009) which prompts a great deal of concern for the impacts on coral reef assemblages in the western Atlantic.

Popular with aquarists (Wilson Freshwater et al. 2009), lionfish are highly ornate predatory fishes, with elaborate, feather-like fins. Their dorsal, ventral and anal fins are all tipped with venomous spines that act as conduits for a neurotoxin (Cohen and Olek 1989) that causes pain in humans but is not known to be fatal. The venom is not used in hunting and is presumed to be for defensive purposes although very little is known about predation on lionfish in their home range (Morris and Whitfield 2009). The fish are gonochoristic asynchronous batch spawners and can produce eggs

continuously when conditions are favourable. The eggs form a floating mass, covered in a gelatinous matrix that may entrap sperm and increase fertilisation rate (Morris et al. 2011), and the larvae have a pelagic duration of 20 to 35 days (Ahrenholz and Morris 2010), providing an efficient mechanism of dispersal that would stand to the advantage of the invader.

At the time of writing, the final impacts of the invasion are far from clear and there is much work to be done. However, a number of very recent anecdotal reports from members of the Gulf and Caribbean Fisheries Institute suggest that densities of some longer-established populations have peaked and begun to decline. However, the mechanism of decline is unknown, and whether it results from a lagged predator response on the reefs or in the plankton, genetic problems resulting from a very small (<10) founding population, a stochastic population fluctuation, or something else entirely remains a mystery.

In summary, the first chapter of the present thesis examines the response of herbivore and meso-predator populations to a cessation in trap fishing mortality, using a nine-year series of census data from Bermuda. The second chapter presents a biologically meaningful approach to incorporating mortality processes into mechanistic population models, allowing age- and size-based mortality to act independently, as is the case in nature, and by testing the results against rigorous empirical results. The third chapter develops a novel method for estimating growth parameters from mark-recapture data that performs better than the most commonly used method when few samples are available, as is commonly the case in reef fish tagging studies. The final chapter uses stable isotope approaches to characterise the shifting trophic position of lionfish in the Bahamas, and to examine differentials in prey selection and competition within and among habitats. The thesis finishes with a discussion of a number of research questions that remain unanswered by the present work, suggesting directions for future research within these fascinating fields.

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2

Density-dependent response of coral reef herbivores and meso-predators to a fishery closure

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Abstract

Traps are one of the most widely used artisanal fishing gears in the Caribbean, and have been shown capable of decimating reef fish populations with cascading impacts on ecosystem function.

Recognising the dramatic demise in fish stocks that was occurring on its reefs, Bermuda imposed a ban on trapping in 1990, although hook and line fishing was not banned and continued to suppress populations of large piscivores. We use a time series of census data to examine the response of key herbivore and mesopredator populations to the release from fishing pressure. We find that the biomass of parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) increased by factors of 2.67 and 3.37 respectively in nine years, with substantial recoveries occurring in six species but not in striped parrotfish (*Scarus iserti*). There was a significant increase in body size of all herbivores except blue tang (*Acanthurus coeruleus*) and a dramatic shift in the sex ratios of all parrotfishes, where the average proportion of males increased nine-fold. Despite the recovery in adult biomass, there was no increase in abundance of juvenile parrotfishes, but we find a greater than six-fold increase in the biomass of trumpetfish (*Aulostomus maculatus*) which is a voracious predator of small fishes. We conclude that trumpetfish may have exhibited a numerical response to prey enrichment, and that stock-recruitment relationships in closed fish populations may be obscured by compensatory responses in predation.

Keywords: recovery dynamics, density dependence, numerical response, post-settlement mortality, trap fishing, sex skews

Introduction

Fisheries science traditionally has been concerned with maximising the yield from individual populations, but in recent years the research focus has shifted towards ecosystem based management (EBM) where the ecological contribution of species is considered when formulating management strategies (Francis et al. 2007, Hilborn 2011, Kellner et al. 2011). The EBM approach is particularly apposite in coral reef systems, where many fishes contribute directly to processes that are vital in maintaining ecosystem function. One such process is grazing, which plays a pivotal role in controlling the growth of reef macroalgae (Williams et al. 2001) that may otherwise negatively impact on the ability of corals to maintain benthic dominance and of reefs to recover from disturbance (Mumby et al. 2006b). Until the early 1980s, the primary grazer in the wider Caribbean was the long-spined sea urchin, *Diadema antillarum*, but the abrupt region-wide decline of the species (Lessios 1988) has left herbivorous fishes in the role of most important grazers (Mumby et al. 2006b). For this reason it is vital that fishing impacts on herbivores are understood so that management plans can be formulated to enhance ecosystem resilience rather than to diminish it.

Traps are one of the most commonly used fishing gears on Caribbean reefs (Gobert 1998) and their depletory effects on fish populations are well documented (Ferry and Kohler 1987, Wolff et al. 1999, Hawkins and Roberts 2004, Hawkins et al. 2007). In an attempt to address the severe decline in fish stocks that had occurred in the 1970s and 1980s, Bermuda implemented a total ban on the use of fish traps in April 1990 (Luckhurst 1999) but allowed hook-and-line fishing to continue. Traps are relatively non-selective gears and retain species from all guilds, including large numbers of herbivores (Koslow et al. 1994, Hawkins et al. 2007) whereas hook-and-line fishing tends to select for piscivores (Dalzell 1996). The continuation of the Bermuda hook-and-line fishery after the trapping ban took effect (Trott and Luckhurst 2007) meant that populations of many predators experienced ongoing control by fishing whereas herbivore populations were released.

Bermuda offers a number of advantages for teasing apart reef fish demographic processes that are often inextricable, and to testing theories of predator response to prey enrichment. Crucially, the fact that Bermuda's closest neighbouring reefs lie over 1000 km away (Figure 2.1) means that observations of demographic processes on the reefs are unlikely to be confounded by those occurring on neighbouring reefs. In the study of population dynamics, local populations are considered to be regulated by density-dependent (DD) processes operating on at least one of the four vital rates, namely immigration, emigration, recruitment and mortality (Hixon 1998).

Immigration and emigration may be discounted in Bermuda because adult reef herbivores do not

migrate vast distances across open seas. The third vital rate, recruitment, is mostly internal in Bermuda, with Schultz and Cowen (1994) demonstrating that although there was periodic larval import to the archipelago it was not sufficient to sustain local fish populations. This facilitates the exploration of stock-recruitment relationships that are commonly obscured in open populations where local recruitment is not driven by local reproduction.

The fourth vital rate, mortality, can be divided into fishing and natural mortality, and the implementation of a ban on trapping releases herbivores from the former. Natural mortality in reef fishes is commonly applied in a DD manner through the action of predation (Caley et al. 1996, Hixon and Jones 2005, White et al. 2010) and the ongoing fishing of large piscivores in Bermuda (Trott and Luckhurst 2007) releases herbivores from predation in the adult stages. However, meso-predators may continue to inflict mortality on early post-settlement stages of herbivores, highlighting a further advantage of the Bermuda dataset: after the fishing ban, some meso-predators, such as coney (*Cephalopholis fulva*) continued to be heavily fished by hook-and-line (Trott and Luckhurst 2007), thereby amplifying any response to prey enrichment by unfished meso-predators, such as trumpetfish (*Aulostomus maculatus*).

Taking advantage of the ‘natural experiments’ arising in the reef system of Bermuda, we quantify the response of herbivores and meso-predators to a cessation of trap fishing, asking five specific questions:

1. *Response of herbivore biomass to the trapping ban*

Scarids (parrotfishes) and acanthurids (surgeonfishes) were not explicit fisheries targets in Bermuda (B.E.L., pers. comm.) and were caught incidentally in traps. Some workers have suggested that non-target fishes gain little benefit from the imposition of fishing restrictions (Micheli et al. 2004) and we test this assertion by examining whether changes in scarid and acanthurid biomass occurred after the Bermuda fishery closure. We examine the data at both family and species level.

2. *Response of herbivore body size to the trapping ban*

Given that fishing tends to reduce the body size of fish in a population (Jennings and Lock 1996), we test whether the mean size of scarids and acanthurids changed after the fishery closure.

3. *Response of scarid sex ratios to the trapping ban*

The most common scarids in Bermuda, and much of the wider Caribbean, belong to the genera *Scarus* and *Sparisoma* (Hawkins and Roberts 2003). These genera are sexually dimorphous

sequential hermaphrodites with males tending to be larger than females (Winn and Bardach 1957). Since larger bodied individuals are more heavily impacted by fishing (Russ 1991), sex ratios of sexually dimorphous fishes may become skewed (Munro and Williams 1985, Buxton 1992, McGovern et al. 1998), having impacts that extend beyond reduction in population size (Jennings and Lock 1996). We examine changes in scarid sex ratios after the fishery closure.

4. *Response of scarid recruit abundance to changes in adult biomass*

A substantial increase in adult herbivore biomass in a closed population such as Bermuda (Schultz and Cowen 1994) should drive a commensurate increase in larval output. Although our dataset does not allow us to examine changes in mortality occurring during the planktonic stage, we test whether any changes in the post-settlement stage (here, up to 5 cm fork length) may be discerned.

5. *Response of fished and unfished meso-predators to the trapping ban*

In addition to regulation through mortality during planktonic stages, scarid populations may be regulated through post-settlement predation, such that an increase in larval output may not necessarily enhance recruitment if compensatory response occurs in mesopredators (Caley et al. 1996). As a result of heavy fishing, Bermudan populations of most Serranid (grouper), Lutjanid (snapper) and Carangid (jack/trevally) meso-predators are low (B.E.L., unpublished data). In fact, in the wake of the trapping ban, fishing pressure on *Cephalopholis fulva* (coney) actually increased dramatically throughout the 1990s as a result of a burgeoning hook-and-line fishery (Trott and Luckhurst 2007). However, not all meso-predators are fisheries targets, and the lack of large piscivores in Bermuda may explicate a response in such species that may otherwise have been obscured by top-down control. A key example is the trumpetfish, *Aulostomus maculatus*, which is a voracious predator of larval and post-larval stage fishes (Randall 1967). Characterised by an exceedingly slender, elongate body, *A. maculatus* often enter fish traps but are rarely retained as they easily swim through the mesh when the trap is hauled (S.O.F., pers. obs.). Fishing mortality for *A. maculatus* in Bermuda would have been negligible prior to the ban, meaning that the population would not be expected to respond directly to a release from fishing pressure and observed changes in biomass are likely attributable to other factors.

There are four ways in which predators may respond to prey enrichment and exert direct DD mortality (White et al. 2010): aggregative responses (Hassell and May 1974), functional responses (Holling 1959), developmental responses (Murdoch 1971) and numerical responses (Holling 1959). Although we cannot use our dataset to examine behavioural (aggregative or functional) nor developmental responses in meso-predators, we examine the census data for evidence of a

numerical response in *C. fulva* (fished) and *A. maculatus* (unfished), which, to our knowledge, has not previously been shown empirically in reef fish (White et al. 2010).

Methods

Study site and survey protocol

Bermuda is a sub-tropical archipelago of 181 islands in the north Atlantic, located approximately 1000 km east of the continental USA. The islands lie towards the south east of an extensive reef platform, and the locations of the three survey sites are shown in Figure 2.1. The reef area at each site was larger than 10^3 m^2 and was considered relatively homogenous.

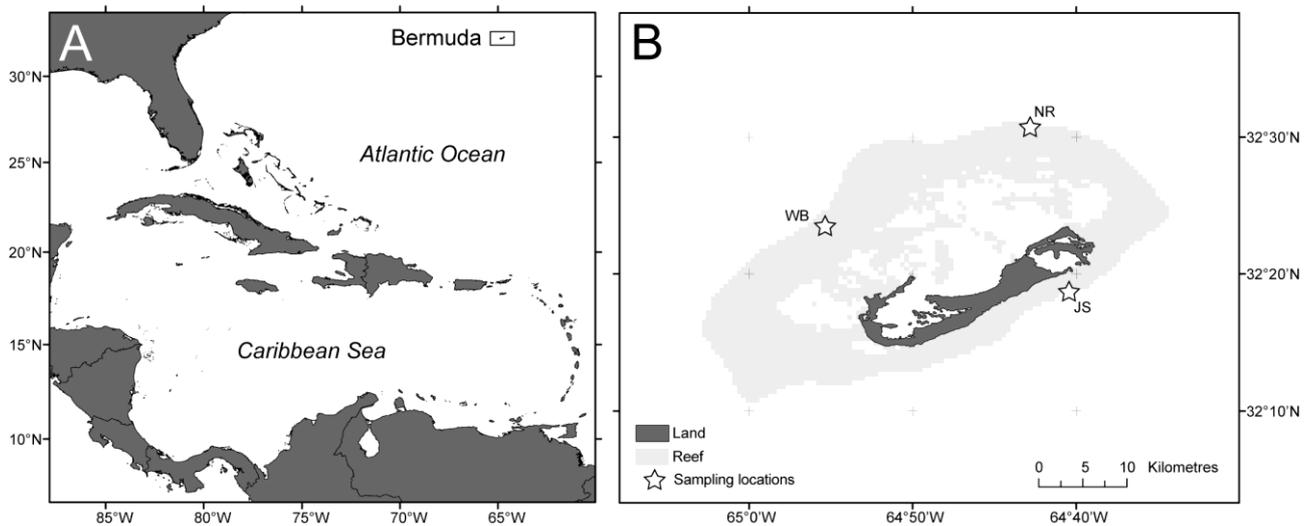


Figure 2.1 Position of Bermuda in the western Atlantic Ocean (A) and the three sampling locations on the Bermuda reef platform (B). NR, North Rock; JS, John Smith's Bay; WB, West Blue Cut. National political boundaries reproduced from the World Vector Shoreline dataset, coral reef locations from Reefs at Risk Revisited, World Resources Institute 2011.

Data gathering began in June 1991, 14 months after the implementation of the trapping ban.

Underwater fish censuses were conducted following the stationary visual census method of Bohnsack and Bannerot (1986). All censuses were conducted at depths between 9 and 12 m and between 1000 and 1500 hours. Stationary surveys were located haphazardly at each site. Using a tape measure, the diver visualised a cylinder of radius 7.5 m extending from the substrate to the surface. Rotating slowly within the cylinder, the diver initially identified the species observed within the cylinder, and then recorded the abundance and body size of individuals, taking 10-15 minutes to conduct each survey. Body sizes were recorded as fork length (FL) to the nearest centimetre. To minimise identification error, the data for scarids smaller than 5 cm were pooled. Further details of the survey protocols and site description are given in Luckhurst (1999). To remove noise created by variations in observer bias, all surveys were carried out by the same diver.

Data collected during 984 underwater censuses conducted by B.E.L. between June 1991 and December 1999 at three sites, John Smith’s Bay, North Rock and West Blue Cut (Figure 2.1 and Table 2.1). Additional surveys were conducted between 1991 and 1994 at a fourth site, South West Breaker, and although these data have been included in preliminary analyses of the dataset (e.g., Luckhurst 1999) they have been excluded in the present work as they do not span the entire study timeframe. The results from each of the outlined research questions are presented in turn.

Table 2.1 Total number of surveys conducted at each site in each year and (in parentheses) total survey time in minutes.

Site	1991	1992	1993	1994	1995	1996	1997	1998	1999
John Smith’s Bay	62 (1081)	30 (486)	15 (216)	92 (1167)	32 (375)	24 (273)	8 (89)	8 (81)	0 (0)
North Rock	61 (977)	40 (628)	23 (305)	96 (1197)	56 (680)	48 (542)	8 (84)	0 (0)	16 (174)
West Blue Cut	70 (1170)	40 (636)	23 (290)	96 (1275)	56 (722)	40 (462)	8 (100)	0 (0)	32 (350)

Data analysis

Biomass was calculated using empirical length-to-weight conversion parameters (Froese and Pauly 2011). Duration varied among surveys and so biomass data were standardised to one minute periods, hereafter referred to as standardised biomass. Models were fitted using nonlinear least squares (NLS) which assume Gaussian error distribution. Because our data were zero-bounded they tended to be right skewed and so the response variable underwent log+1 transformation and residuals were subsequently checked for normality using quantile-quantile plots of standardised residuals versus fitted values (Crawley 2007).

Three production models (Table 2.2) were assessed to determine which best fit the data, using nonlinear least squares fitting in the R package, nls2 (Grothendieck, 2011). First, a simple linear model was fitted, followed by a Ricker model which allows for an initial peak followed by a subsequent decline (McClanahan et al. 2007), and finally a logistic model which reaches an asymptote at carrying capacity, achieving its maximum growth rate at half that capacity (Crawley 2007). To assess the goodness of fit, log likelihood ratio tests were carried out, whereby the likelihood of each candidate model was tested against that of a null model, here a straight line with a slope of zero whose intercept is the general mean of the response variable. When multiple models

were deemed to be ‘likely’ at a 95% confidence level, as will often be the case, the optimal model was chosen using Akaike’s Information Criterion (AIC), which allows models with varying numbers of parameters to be equitably compared. AIC penalises the inclusion of additional parameters because a model with more parameters is likely to explain a greater proportion of the variance but at the expense of explanatory power (Crawley 2007). When models are within two AIC values of each other it is not possible to choose one over the other based on the data (Burnham and Anderson, 2002) and so both models are presented.

Table 2.2 Population growth models fitted to field data

Model	Formula	Parameters
Linear	$a + bt$	a is the intercept, b is the slope and t is time, expressed as years since fishery closure
Ricker	$N_0 + (bt)e^{-kt}$	N_0 is initial population size, b is the slope of the regression curve at t_0 , e is the base of the natural logarithm and k is the initial rate of decline
Logistic	$a + \left(\frac{b - a}{1 + e^{r(d-t)}} \right)$	a and b are the left and right hand asymptotes, r is the growth rate and d is the inflexion point of the curve

Results

1. Response of herbivore biomass to the trapping ban

Changes in herbivore biomass over the study period were examined at two taxonomic levels, by family (Figure 2.2 and Table 2.3) and by species (Figure 2.3 and Table 2.4).

Changes in biomass by family

The biomass of scarids increased by a factor of 2.67 in the nine years following the fishing ban (Figure 2.2A) and the biomass of acanthurids increased by a factor of 3.27 (Figure 2.2B). The best fitting model for both taxa was logistic (Table 2.3). Not only was the proportional increase in acanthurid biomass greater than that of scarids, it occurred more swiftly; the acanthurid model reaches an asymptote after around four years whereas the scarid model requires around eight years. The absolute biomass of scarids however was larger than that of acanthurids at all times.

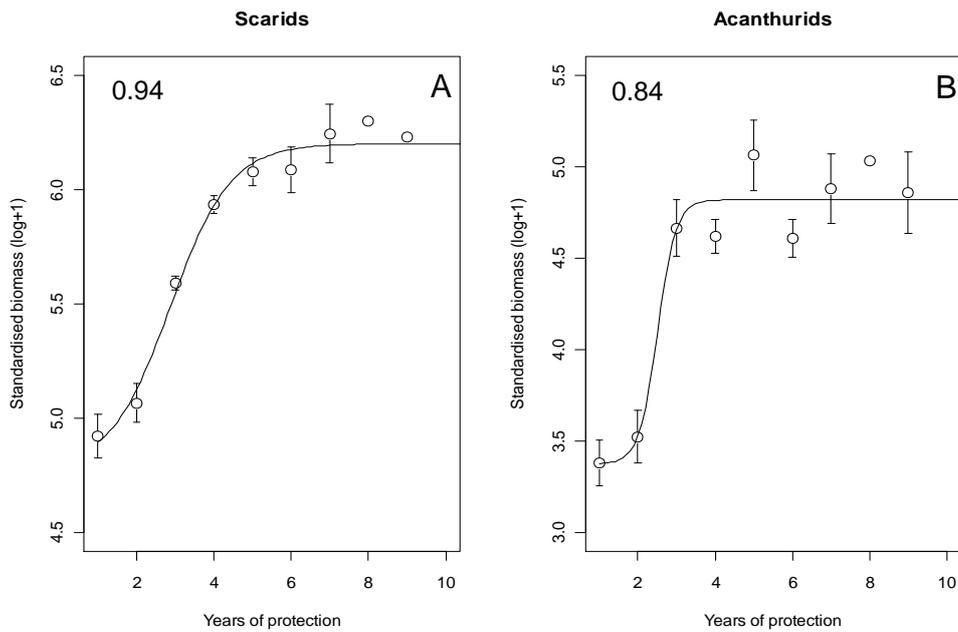


Figure 2.2 Changes in biomass by family group over a 9 year period, using census data commencing approximately one year after the cessation of trapping. Markers and bars show means and standard errors of field data. The best fitting model for both families was logistic. Note that the vertical scale varies.

Table 2.3 Changes in biomass of two major herbivore families, plus parameter values estimated during model fitting. Likelihood (95% level) and AIC (in parentheses) for each fit are shown below each parameter set. Best fitting parameters are shown in bold. Recovery factor is the proportional increase between the means from 1991 and 1999. Equations are shown in Table 2.2.

Family	Recovery factor	Linear		Ricker			Logistic			
		<i>a</i>	<i>b</i>	N_0	<i>b</i>	<i>k</i>	<i>A</i>	<i>B</i>	<i>r</i>	<i>d</i>
Scaridae	2.67	4.93	0.18	4.27	0.62	0.11	4.77	1.42	1.29	2.87
		$P < 0.001$ (3.13)		$P < 0.001$ (-17.66)			$P < 0.001$ (-22.75)			
Acanthuridae	3.27	3.57	0.19	2.37	1.04	0.15	3.38	1.44	4.21	2.51
		$P < 0.001$ (32.99)		$P < 0.001$ (19.38)			$P < 0.001$ (11.59)			

Changes in biomass by species

Species-level data were examined for the most abundant grazers (five scarids and two acanthurids). Two genera of scarids were included, represented by the species *Scarus vetula* (queen), *Sc. taeniopterus* (princess), *Sc. iserti* (striped), *Sparisoma viride* (stoplight) and *Sp. aurofrenatum* (redband). The most abundant acanthurids were *Acanthurus bahianus* (ocean surgeonfish) and *A. coeruleus* (blue tang). With the exception of *Sc. iserti*, all of the grazers showed substantial increases in biomass (Figure 2.3). Increases were best modelled by logistic functions, except for *A. coeruleus* whose best fitting model was the Ricker function (Table 2.3) but the data for *A. coeruleus* are noisy and the fit is extremely poor (Figure 2.3G).

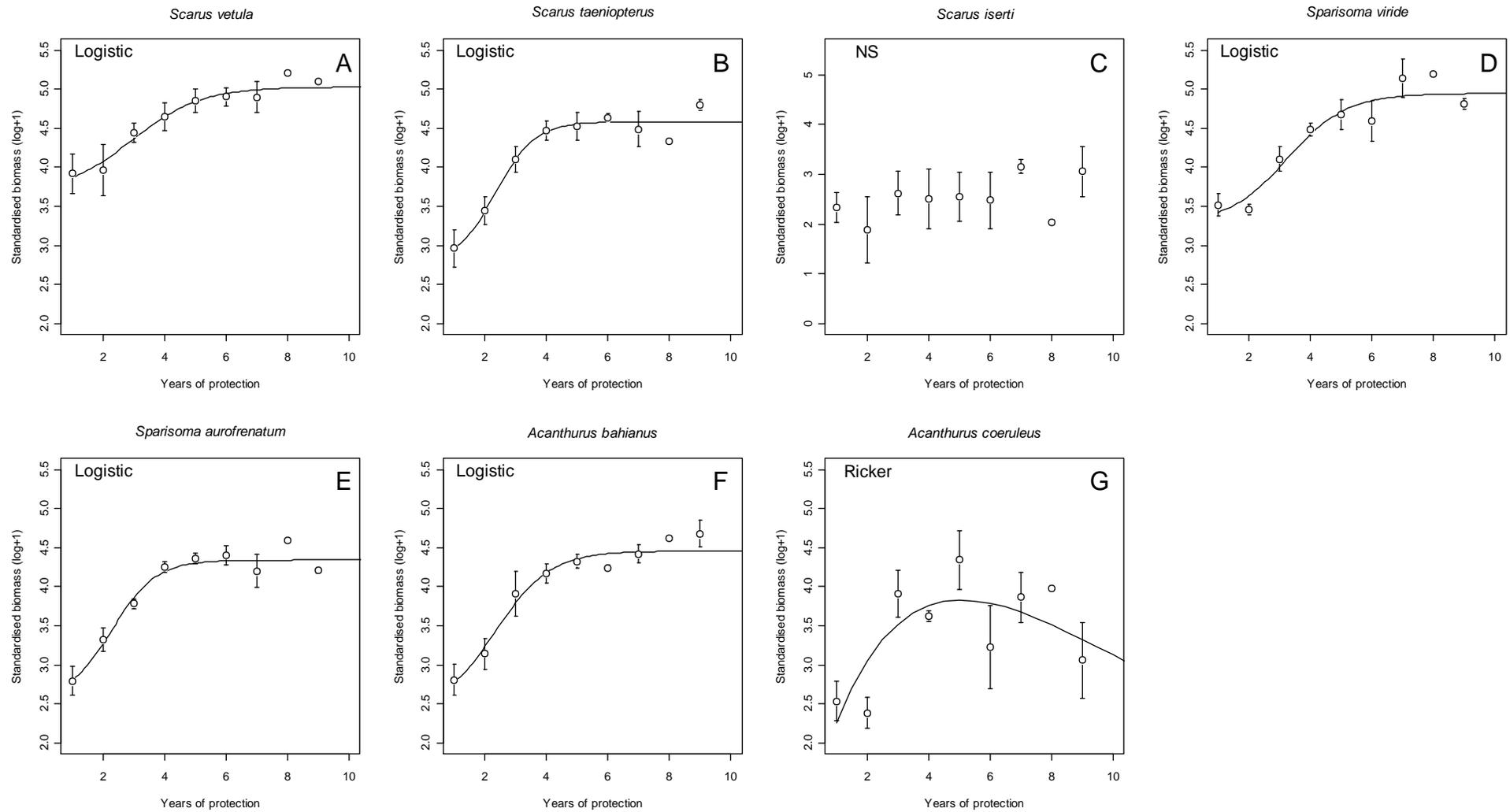


Figure 2.3 Changes in biomass by species, using census data commencing approximately one year after the cessation of trapping. The best fitting model for each species is specified in each panel. ‘NS’ indicates no significant model fit. Markers and bars show means and standard errors of the field data.

Table 2.4 Changes in biomass of seven common herbivore species, and parameter values estimated during model fitting. Likelihood (95% level) and AIC (in parentheses) are shown below each parameter set. Best fitting model parameters are shown in bold type. Recovery factor is the proportional increase between the mean values from 1991 and 1999.

Species	Recovery factor	Linear		Ricker			Logistic			
		<i>a</i>	<i>b</i>	<i>N</i> ₀	<i>b</i>	<i>k</i>	<i>A</i>	<i>B</i>	<i>r</i>	<i>D</i>
<i>Scarus Vetula</i>	2.08	3.85	0.16	3.45	0.41	0.09	3.67	1.36	0.89	2.94
		<i>P</i> <0.001 (17.42)		<i>P</i> <0.001 (15.94)			<i>P</i> <0.001 (17.31)			
<i>Scarus taeniopterus</i>	5.24	3.21	0.21	2.04	1.02	0.14	2.75	1.83	1.55	2.33
		<i>P</i> <0.001 (28.79)		<i>P</i> <0.001 (12.19)			<i>P</i> <0.001 (10.98)			
<i>Scarus iserti</i>	NA	2.07	0.09	2.06	0.11	0.01	NC			
		<i>P</i> =0.132 (58.76)		<i>P</i> =0.307 (60.76)			NC			
<i>Sparisoma viride</i>	2.68	3.36	0.22	2.81	0.57	0.09	3.27	1.68	1.03	2.23
		<i>P</i> <0.001 (22.61)		<i>P</i> <0.001 (18.62)			<i>P</i> <0.001 (18.16)			
<i>Sparisoma aurofrenatum</i>	3.18	3.08	0.19	1.81	1.08	0.16	2.55	1.79	1.4	2.28
		<i>P</i> <0.001 (26.48)		<i>P</i> <0.001 (4.28)			<i>P</i> <0.001 (1.44)			
<i>Acanthurus bahianus</i>	5.68	2.92	0.23	2.07	0.8	0.12	2.4	2.1	1.12	2.33
		<i>P</i> <0.001 (22.56)		<i>P</i> <0.001 (11.66)			<i>P</i> <0.001 (12.34)			
<i>Acanthurus coeruleus</i>	8.5	2.85	0.12	1.02	1.5	0.2	NC			
		<i>P</i> =0.076 (59.57)		<i>P</i> <0.001 (53.01)			NC			

na, not applicable; nc, non-convergence by fitting algorithm

2. Response of herbivore body size to the trapping ban

Changes in mean body size were analysed by species but the data were noisy and a good deal of variance was unexplained by the fitting of the models (Figure 2.4). However, for six out of the seven herbivores examined, the difference in mean size increased significantly between 1991 and 1999 (Table 2.5). Within the scarids, the two smallest bodied species, *Scarus iserti* and *Sparisoma aurofrenatum*, respectively displayed the greatest (recovery factor = 3.4) and the least (recovery factor = 1) increases in size of all herbivores.

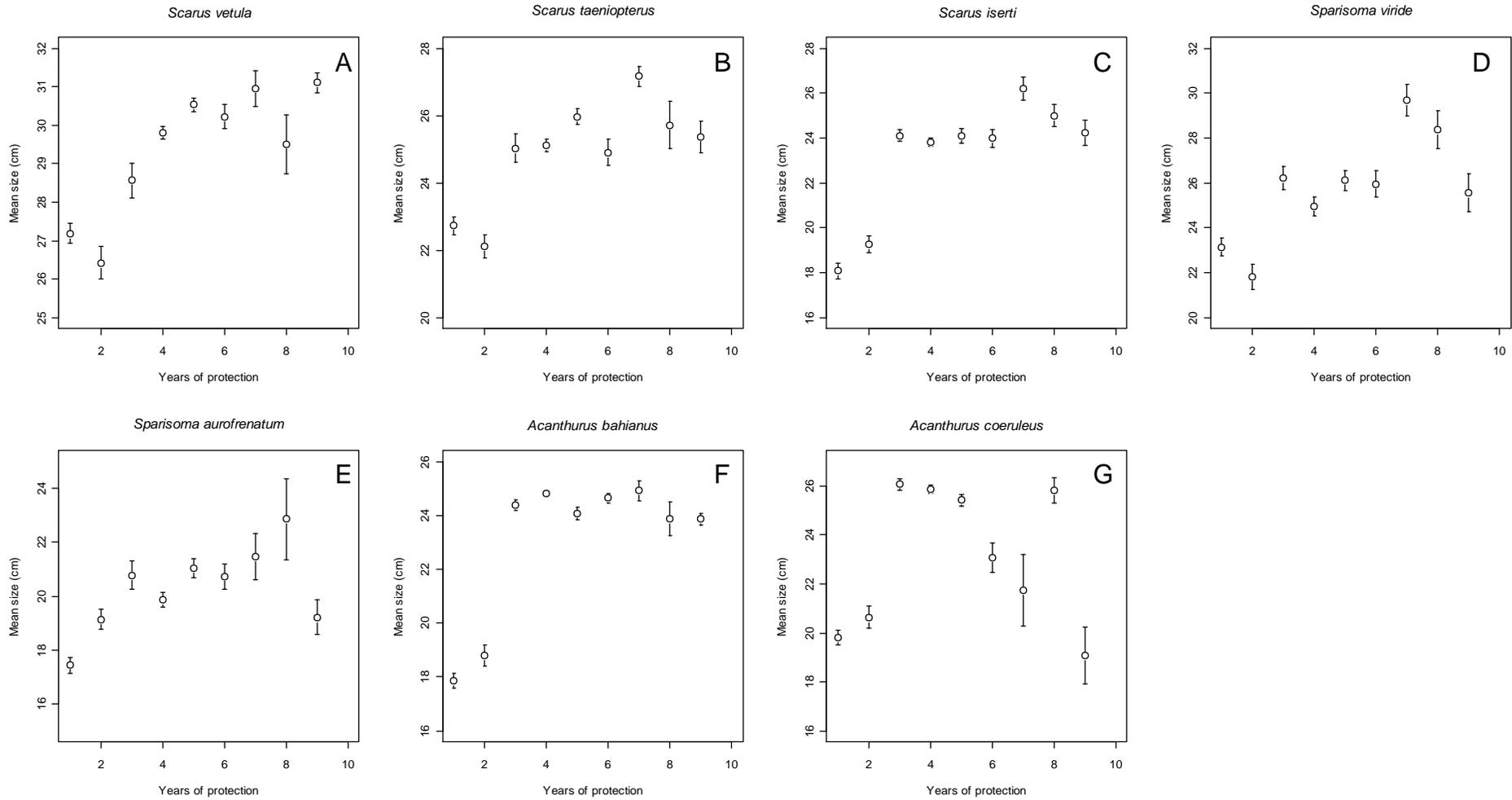


Figure 2.4 Changes in mean body size of scarids and acanthurids across the study period, using data commencing approximately one year after the cessation of trapping. Markers and bars show means and standard errors of the field data.

Table 2.5 Changes in mean body size from 1991 to 1999 for seven common reef herbivores. Recovery factor is the proportional increase between the mean values from 1991 and 1999.

Species	Mean size 1991 (+ s.e.)	Mean size 1999 (+ s.e.)	<i>t</i> -test results	Recovery factor
<i>Scarus vetula</i>	27.19 (0.26)	31.11 (0.25)	$t_{[168]} = 10.33;$ $P < 0.001$	1.4
<i>Scarus taeniopterus</i>	22.73 (0.27)	25.36 (0.47)	$t_{[83]} = 4.69;$ $P < 0.001$	1.2
<i>Scarus iserti</i>	18.08 (0.34)	24.23 (0.57)	$t_{[60]} = 7.26;$ $P < 0.001$	3.4
<i>Sparisoma viride</i>	23.13 (0.39)	25.55 (0.85)	$t_{[72]} = 2.52;$ $P = 0.014$	1.1
<i>Sparisoma aurofrenatum</i>	17.43 (0.29)	19.22 (0.63)	$t_{[66]} = 2.47;$ $P = 0.015$	1
<i>Acanthurus bahianus</i>	17.85 (0.27)	23.87 (0.21)	$t_{[191]} = 16.34;$ $P < 0.001$	3.3
<i>Acanthurus coeruleus</i>	19.81 (0.29)	19.08 (1.15)	$t_{[24]} = 0.421;$ $P = 0.677$	<i>ns</i>

ns, not significantly different from zero; all tests were two tailed

3. Response of scarid sex ratios to the trapping ban

All scarid populations underwent large changes in sex ratios with the proportions of terminal phase males increasing dramatically (Figure 2.5). For *Sc. taeniopterus* the best fit was given by the Ricker function but for the remaining scarids the increase was best described by the logistic function (Table 2.6). After an initial lag, extremely high male proportions were consistently recorded for *Scarus iserti* (Figure 2.5C).

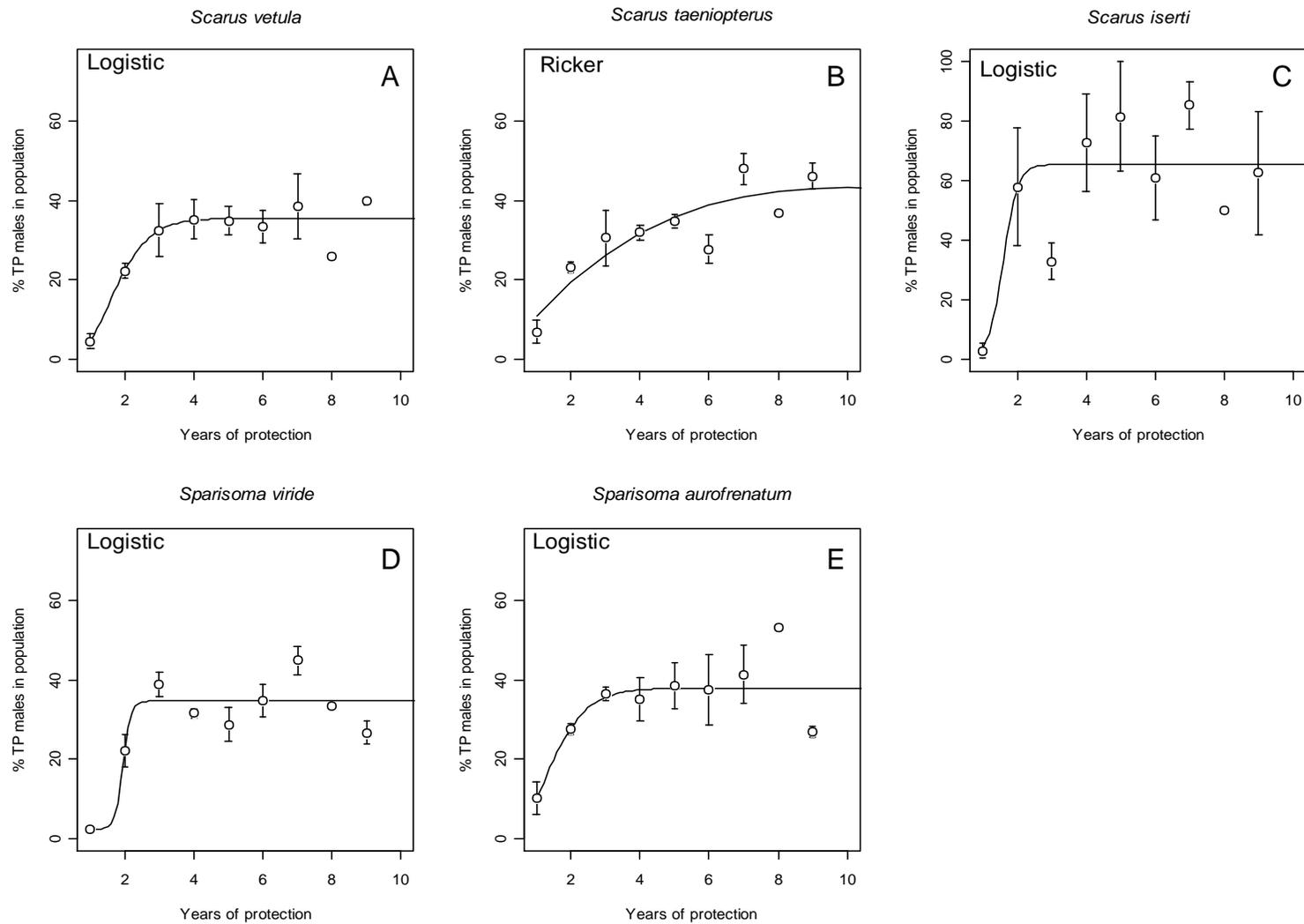


Figure 2.5 Changes in the sex ratios of five scarid species over time, expressed as percentage of males in the population. Individuals smaller than 5 cm were not included in the analysis. The best fitting model for each species is specified in the appropriate panel. Markers and bars show means and standard errors of the field data.

Table 2.6 Parameter values estimated for five scarids during model fitting to sex ratio data. Likelihood (95% level) and AIC (in parentheses) are shown below each parameter set. Best fitting model parameters are shown in bold type. Recovery factor is the proportional increase between the mean values from 1991 and 1999.

Species	Recovery factor	Linear		Ricker			Logistic			
		<i>a</i>	<i>b</i>	N_0	<i>b</i>	<i>k</i>	<i>a</i>	<i>b</i>	<i>r</i>	<i>d</i>
<i>Scarus vetula</i>	7.83	14.51	3.29	0	14.48	0.14	-7.43	42.99	1.77	1.54
		<i>P</i> <0.001 (183.11)			<i>P</i> <0.001 (175.19)			<i>P</i> <0.001 (171.96)		
<i>Scarus taeniopterus</i>	5.64	11.84	4.14	0.29	11.71	0.11	2.1	38.97	0.76	2.28
		<i>P</i> <0.001 (173.49)			<i>P</i> <0.001 (171.88)			<i>P</i> <0.001 (177.11)		
<i>Scarus Iserti</i>	20.01	26.28	6.63	0	27.56	0.14	0.1	65.39	4.76	1.59
		<i>P</i> <0.001 (233.01)			<i>P</i> <0.001 (235)			<i>P</i> <0.001 (231)		
<i>Sparisoma viride</i>	9.92	15.48	2.98	0	15.46	0.16	2.44	32.27	9.1	1.95
		<i>P</i> <0.001 (187.29)			<i>P</i> <0.001 (176.76)			<i>P</i> <0.001 (169.83)		
<i>Sparisoma aurofrenatum</i>	1.65	20.98	2.59	0	18.55	0.17	-10.6	48.96	1.63	1.17
		<i>P</i> <0.001 (189.07)			<i>P</i> <0.001 (180.52)			<i>P</i> <0.001 (175)		

4. Response of scarid recruit abundance to changes in adult biomass

Like most spawning fishes, the reproductive capacity of scarids is a function of body mass (Muñoz and Warner 2004), yet despite the magnitude of the increase in adult biomass, the combined abundance of all scarids smaller than 5 cm shows no increase during the study period (Figure 2.6). In fact, a linear regression of abundance on time implies that the abundance of recruits actually decreased slightly during the study period (Slope = -0.04; $F_{[1, 330]} = 5.35$; $P = 0.03$) although this pattern may be disproportionately influenced by the large value in year 3.

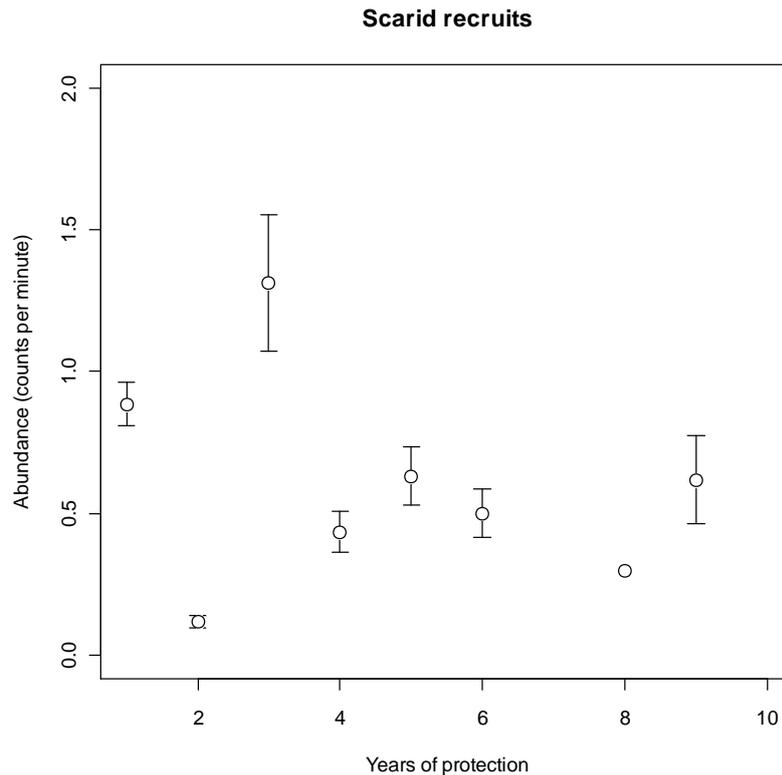


Figure 2.6 Abundance of recruits (< 5cm) of all scarid species combined, showing no consistent increase in the number of small fish found on the reefs across the nine year study period. Markers and bars show means and standard errors of the field data.

5. Responses of fished and unfished meso-predators to the trapping ban

The biomass of *Cephalopholis fulva* (coney) did not change significantly (linear regression: $F_{[1,22]} = 0.526$; $P = 0.476$) during the study period (Figure 2.7A). Although *C. fulva* would have been released from trapping pressure by the fishing ban, hook-and-line fishing pressure increased for the species through the decade (Trott and Luckhurst 2007). Conversely, the biomass of *Aulostomus maculatus* increased by a factor of 6.57 over the 9 year period (Figure 2.7B). Indeed, the logistic model (log likelihood ratio test: $P < 0.001$) fitted to the *A. maculatus* data does not reach its asymptote by the end of the study period, suggesting that the biomass may have continued to increase after the data-gathering period.

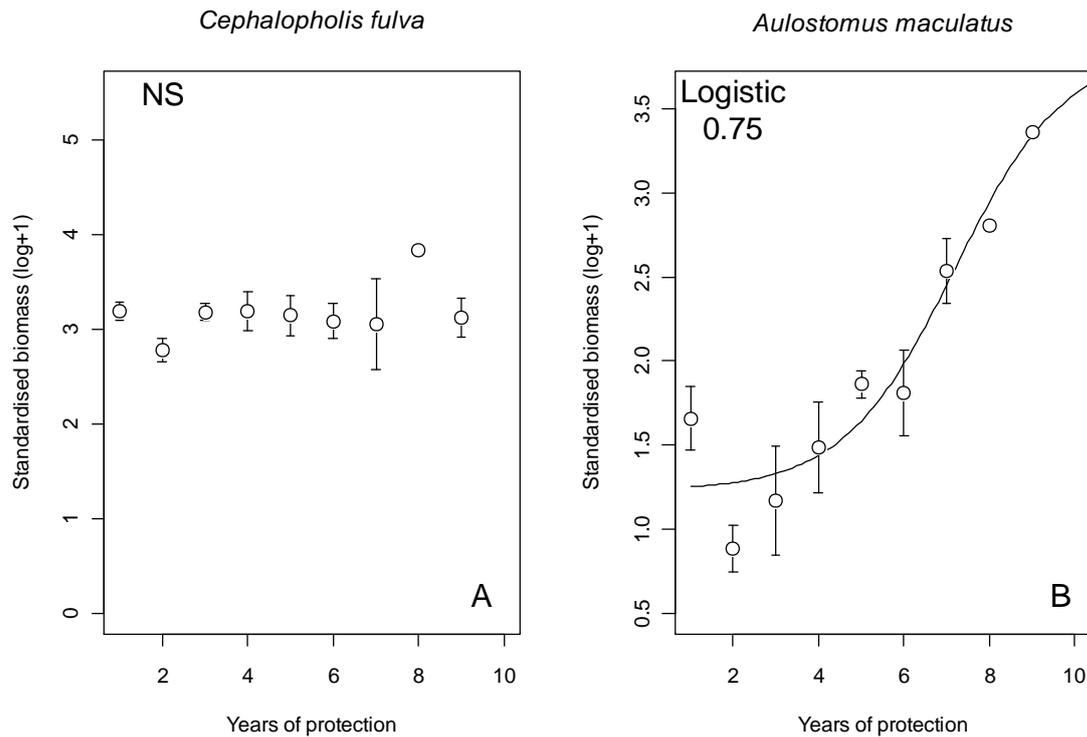


Figure 2.7 Biomass of two common meso-predators on Bermudan reefs in the nine-year period following the fishery closure. No significant change in biomass was observed for *Cephalopholis fulva*. Markers and bars show means and standard errors of the field data.

Discussion

Our results provide important insight into the response to fishing of the dominant reef herbivores and unique insight into the processes driving population dynamics of reef fish. We consider each in turn.

Impacts of fishing on parrotfishes

In sequential hermaphrodites, the triggers of sex change are poorly understood (Muñoz and Warner 2004) and it could be hypothesised that the impacts of size-selective fishing may be mitigated by a compensatory response, whereby the removal of large males triggers females to change sex and grow, and a drop in DD mortality facilitates increased survival of juvenile females to replenish the population. However, our data clearly show that mean body sizes and sex ratios of sequential hermaphrodites are profoundly affected by fishing. Although there has been limited work in this field, our findings support those of other studies (e.g., Hawkins and Roberts 2003).

Hermaphroditism is common in reef fishes, and the skewing of sex ratios must act to reduce reproductive capacity, exacerbating population decline induced by trap fisheries.

Scarus iserti was the only parrotfish not to show an increase in biomass following the fishing ban. This result might have been expected if it were the smallest-bodied scarid represented as it may not have been as heavily impacted by fishing as other species, but *Sparisoma aurofrenatum* is of similar body length in Bermuda and yet showed a strong recovery. However, for a given length, fish of lower dorso-ventral height are less likely to be retained by traps as they can squeeze through the bars more readily (Robichaud et al. 1999), and subjecting previously published data from the Bahamas (Mumby et al. 2006a) to further testing shows that the ratio of height to length is indeed greater in *Sp. aurofrenatum* (0.37) than in *Sc. iserti* (0.34) (U-test, $P = 0,03$, 1-tailed). Interestingly, in Barbados, where traps are used extensively, *Sc. iserti* dominates the parrotfish community (P.J.M., unpubl. data).

It is intriguing that analysis of the biomass data alone would imply *Sc. iserti* was not affected the fishing ban, yet the mean body length of the species increases in the dataset. Two possible explanations for the paradox are that it is driven by inter-specific facilitation or by intra-specific sexual restructuring. *Sc. iserti* grazes predominantly on algal turfs which are competitively inferior to macroalgae such as *Dictyota* spp. (Mumby et al. 2005) but these macroalgae are in turn suppressed by grazing of large scarids (Mumby et al. 2007), releasing the turfs from competitive pressure. The population growth seen in the other scarid species will have resulted in a large increase in grazing, which would be expected to encourage the growth of algal turfs, the preferred food resource of *Sc. iserti*, thereby facilitating an increase in mean body size. Of course, for a population to gain in mean body size without increasing in biomass necessitates a decrease in abundance, which could be driven by increased inter-specific competition for space in these highly territorial fish (Mumby and Wabnitz 2002).

An alternative explanation is offered by the extraordinarily high proportions of terminal phase males, peaking in year 7 at over 80%. Male *Sc. iserti* tend to be larger than females, and a shift in the sex ratios in favour of terminal phase males would indeed produce an increase in mean size, but why such a dramatic sexual restructuring should have occurred remains a mystery. The cues that drive sex change in scarids are complex and poorly understood (Muñoz and Warner 2004) but may in time provide insight into the response of the *Sc. iserti* population we report here.

In an analysis of long term recovery trends of fish populations following the closure of a fishery in Kenya, McClanahan et al. (2007) found that scarid and acanthurid biomass took, respectively, ~20 years and >35 years to recover from fishing when predators were protected as well. Our results show that, in the absence of predators, these herbivore families recovered to peak biomass within less than 10 years and less than 5 years respectively (Figure 2.2) although differences in taxa and reef systems do not facilitate robust comparisons of results. Because grazing intensity is an exponential function of body size in parrotfishes (Lokrantz et al. 2008), the dramatic increases both in biomass and in mean body size should have resulted in enhanced grazing intensity on the reefs of Bermuda.

Density-dependence in population recovery from fishing

Although lacking unfished control sites, the Bermudan case study provides a unique opportunity to study the processes underpinning population regulation, by virtue of the fact that prey species were released from trap fishing but most predators were held constant by the ongoing hook and line fishery. Predation is commonly the proximate cause of DD mortality in reef fishes although the ultimate causes may be competition, parasitism and/or disease (White et al. 2010). The strong territoriality displayed by the parrotfishes included in the present analysis (vanRooij et al. 1996, Mumby and Wabnitz 2002) is likely to have driven an increase in intra- and interspecific competition for space, and was probably one of a number of factors that caused the populations to reach asymptotic levels so rapidly.

One of the most interesting findings of our study was the apparent decoupling of the stock-recruitment relationship in Bermudan scarids. The data clearly display a substantial increase in the biomass of post-recruitment scarids (Figure 2.2), and since reproductive output scales with biomass many population models would assume that an increase in adult biomass would result in an increase in recruits in a 'closed' population such as Bermuda. However, the data for the abundance of recruits show no such increase which prompts caution in generally accepting this intuitive assumption. The decoupled response of recruits in our data affords a rare insight to the way in which density dependence may act on the early life stages of reef fish populations.

If a population were regulated in the adult stages, whether through density dependence or fishing, it could of course produce a relatively constant abundance of recruits through constant reproductive output and it would be difficult to tell whether the juveniles themselves experienced DD regulation.. In the Bermuda data, however, we have the opportunity to observe that recruit abundance does not change across a considerable gradient of adult biomass, implying that the recruits must be regulated

independently of the adults. There remain two candidate mechanisms, namely connectivity to regulated populations elsewhere or the local action of DD processes. The nearest reefs to Bermuda lie over 1000 km away across open ocean and Schultz and Cowen (1994) demonstrated that although there was periodic larval import to Bermuda it was not sufficient to sustain local fish populations and that most recruitment was internal. This leaves local density dependent processes as the most likely mechanism and again we are presented with two candidate mechanisms; intra-specific competition and/or predation. The former of these seems unlikely, as none of the authors has ever observed agonistic behaviour towards or among scarid juveniles < 5 cm FL (see also Mumby and Wabnitz 2002). The most parsimonious explanation for the relatively constant recruit abundance over the study period is DD predation, and supporting evidence for this hypothesis is provided by the explosive growth in the population of the mesopredator *Aulostomus maculatus*.

Probably as a result of their high somatic growth rate (e.g., vanRooij et al. 1995) and considerable reproductive output (e.g., vanRooij et al. 1996), our study shows that parrotfishes have the capacity to recover rapidly when released from fishing pressure, but that stock-recruitment relationships may be masked by a DD response in meso-predators. Our study contributes to the body of literature supporting the evolving paradigm that fisheries impacts must be considered at an ecosystem level. Even species which are not primary fisheries targets but are generally regarded as bycatch may be severely affected by non-selective gears, and when such species perform vital ecological roles such as grazing, fisheries must be managed explicitly to mitigate impacts on their populations.

Acknowledgements

The authors wish to thank Iliana Chollett Ordaz for comments and production of maps. The study was supported by funding from the UK Natural Environmental Research Council and Cefas.

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3

Disentangling drivers of trait-dependent mortality: Insights from simulations of a reef fish population

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Abstract

Many significant advances in modeling demographic processes were pioneered in fish population ecology owing to their historical application to fisheries management. Some approaches have been so influential that they are routinely extended to taxa whose life histories differ profoundly from those of the original focus species. One such approach is to model mortality as a constant rate of year-class decline, which disregards changes in individual age or body size. Because such traits may influence mortality, here we challenge the generality of the approach by incorporating it in individual-based simulations of a population of ecologically-important parrotfishes, *Sparisoma viride*. We find that the function performs poorly when confronted with field data, considerably underestimating mortality and overestimating longevity. We then develop functions that partition mortality into trait-dependent processes, combining ecological paradigms (that smaller fish experience elevated predation) with evolutionary theory (that highly reproductive fishes are more likely to senescence). We allow these processes to vary independently within the simulations, as is the case in nature, and in doing so we obtain convincing fits to the field data. In the absence of a universal law of mortality, our study indicates that much may be gained by partitioning mortality by trait.

Keywords: size-escape, trait-dependent, senescence, population dynamics, individual-based simulation, mortality

Introduction

Some of the most groundbreaking work in the quantitative study of wild populations was either developed in the context of, or found early application within, fisheries science. Advances in systems theory and population ecology such as those pioneered by Volterra (1926), von Bertalanffy (1934), and Beverton and Holt (1957) have become mainstays of modern population dynamics, and many approaches developed for modeling populations of traditional fisheries species now find widespread application. One such approach is to model mortality as a trait-independent, time-invariant exponential rate at which year-classes (cohorts) of a population decay (see Beverton and Holt 1957). Highly influential in studying the population dynamics of fisheries species (Vetter 1988) such as tuna (*Thunnus* spp.), this constant mortality approach is now routinely applied to taxa as disparate as woody plants (Cabral and Schurr 2010) and red foxes (Korytin 2002).

The constant mortality approach, hereafter ‘cohort decay’, implicitly assumes that all individuals within a study population have an equal chance of dying at any given time, regardless of individual traits such as age or body size, and the life history characteristics of many traditional, temperate fisheries species lend themselves well to the approach. Populations of these species reproduce annually, creating distinct year classes, and seasonal fluctuations in temperate waters encourage the formation of visible bands in hard body structures from which individual age readily may be estimated (Campana 2001). Many of the species have adopted strategies to moderate predation that may otherwise act disproportionately on smaller individuals. For example, predatory species such as Atlantic cod (*Gadus morhua*) exploit ‘cultivation / depensation’ effects (Walters and Kitchell 2001) whereby adults consume the predators of their own progeny (Pauly et al. 2002). These juveniles often join extremely large aggregations whose schooling behavior is hypothesized further to diminish the effects of predation (Reynolds 1987, Vabø and Nøttestad 1997, Stöcker 1999) and subsequent mortality aptly may be modeled as acting more-or-less randomly on individuals at a constant rate.

However, most taxa exhibit life history characteristics that differ from those of traditional fisheries species, and for many of these, including many other fishes, mortality may be far from constant (Vetter 1988). One such taxon is the parrotfishes (Scaridae), an ecologically important family of coral reef herbivores. As is common in animals that occupy lower trophic levels, parrotfishes invest heavily in reproduction, many species spawning every day, all year round (vanRooij et al. 1996b), undermining the concept of annual cohorts and representing a strikingly different life history

strategy to that of annually reproducing species. As herbivores, the ability of parrotfishes to moderate predation is limited as they cannot utilize ‘cultivation / depensation’ effects, and when groupings occur they are many orders of magnitude smaller (vanRooij et al. 1996a) than those commonly observed in many traditional fisheries species. Rather than true ‘schools’, parrotfish groups may better be described as ‘gregarious aggregations’ (Nikolsky 1963) which have been observed to respond in an uncoordinated manner, even to attacks by predators (Claro et al. 2001) and parrotfishes are thus less capable of insulating themselves from predation than are many traditional fisheries species.

Because parrotfishes play a pivotal role in controlling the growth of seaweeds on coral reefs understanding their population dynamics is critical to managing wild populations in such a way as to maximize coral reef resilience (Mumby et al. 2006) in the face of burgeoning threats from overfishing (Jackson et al. 2001, Newton et al. 2007) and climate change (Hughes et al. 2003, Hoegh-Guldberg et al. 2007). Mortality is one of the vital processes that structures populations (Caswell 2002), and mortality rates of many coral reef fishes previously have been estimated using the traditional cohort decay function (e.g., Choat et al. 2006, Paddock et al. 2009, Heupel et al. 2010, Taylor and McIlwain 2010). However, given the stark contrast between the ecological characteristics of coral reef fishes and traditional fisheries species, we question whether such techniques appositely may be extended and, if not, whether alternative approaches may be suggested. We postulate that the action of mortality is in fact trait-dependent in parrotfishes, as is likely the case in many tropical reef fishes, and that it may vary with age (intrinsic mortality) and body size (extrinsic mortality), which are two of the most fundamental organismal traits (DeAngelis and Huston 1987).

Intrinsic, age-dependent mortality commonly manifests itself through the action of senescence, which may be thought of as age-specific degeneration of fitness (Ricklefs 1998, Reznick et al. 2004). Although the origins of senescence are not well understood, its effects have previously been demonstrated in fish populations (Reznick et al. 2004). Life history theory holds that organisms differentially allocate resources between processes such as growth, somatic maintenance and reproduction in such a way as to maximize fitness (Barnes and Partridge 2003). Investment in reproduction in particular may require costly trade offs in survival, and in model organisms such as *Drosophila* spp. (Sgrò and Partridge 1999) and *Caenorhabditis elegans* (Gems and Riddle 1996), elevated rates of mating cause commensurate increases in aging. The evolution of senescence may therefore be more likely in species that exhibit high spawning rates, such as many reef fishes (Doherty and Fowler 1994), and we contend that aging may be an important driver of mortality in

parrotfishes. This hypothesis would extend to many other tropical reef fishes, and is consistent with the results of Choat et al. (2006), who found that highly-reproductive terminal phase males of the Indo Pacific wrasse, *Cheilinus undulatus*, exhibited shortened lifespans relative to non-transitioning females whose reproductive output is comparatively modest.

Extrinsic, size-dependent mortality is most evident in the form of predation, which is the primary driver of mortality in most fish populations (Lorenzen 1996). It has been shown that smaller fish experience elevated levels of predation (Sogard 1997, Sparre and Venema 1998, Dahlgren and Eggleston 2000, Almany and Webster 2006, Craig et al. 2006, Perez and Munch 2010). However, despite experiencing extremely high levels of juvenile mortality, individuals often outgrow the prey window of many or all of their predators, meaning that predation acts more strongly on smaller individuals than on larger ones (Taylor 2003, Meekan et al. 2006) and we conjecture that parrotfish mortality may vary in a size-dependent manner.

To compare the efficacy of the traditional cohort decay approach against novel methods that incorporate mechanistic trait-dependent mortality processes, we conduct simulations that are parameterized and tested using extensive empirical data from populations of the Caribbean stoplight parrotfish, *Sparisoma viride*. When confronted with field data, we find that simulations incorporating the traditional cohort decay function perform poorly in comparison to simulations built on partially and fully trait-dependent functions. Our study highlights the fact that there is probably no universal law of mortality (Mangel 2008) and that much may be gained by explicitly considering the known biology and ecology of study species when applying ‘off the shelf’ population models.

Methods

Study Animal

Sparisoma viride (Bonnaterre) is a conspicuous member of western Atlantic reef fish communities. An excavating herbivore, *S. viride* removes algae from reef substrates with its beak-like fused teeth, regulating the growth of reef algae, and grazing by *S. viride* plays an important role in maintaining coral recovery and reef development (Mumby & Harborne 2010).

S. viride has a complex and variable life history (Winn and Bardach 1957, vanRooij et al. 1996a, Hawkins and Roberts 2003). When settling to the reef after a planktonic larval phase, all *S. viride* are females (vanRooij et al. 1996a). Sexual maturity begins at a size of around 150 mm, after

which fish may remain female or change sex (vanRooij et al. 1996b). Mature females can join the harems guarded by territorial males in the deeper reef front area, or they can join the roving groups in the shallower areas (Koltes 1993). Multiple females from both deep and shallow groups spawn daily with each territorial male (vanRooij et al. 1996b).

In addition to the non-haremic females, the shallow groups also contain males that have changed sex but have not yet managed to acquire a territory. These ‘bachelor’ males do not spawn, but strategically invest energy in rapid growth (vanRooij et al. 1995) which may maximize their ability to take over a territory should the incumbent male die. The four life phases distinguishable at the study site are thus juveniles, mature females, bachelor males and territorial males, each displaying differing somatic growth rates (vanRooij et al. 1995) which we incorporate in our simulations.

Study Site and Field Data

Field data were gathered at the fringing reef at Karpata in Bonaire, Netherlands Antilles between August 1988 and January 1992. The entire reef at Bonaire is a marine reserve where spear fishing has been banned since 1971 and the *S. viride* population is unexploited (vanRooij et al. 1996b). During the data gathering period, there was no significant variation in adult density or spatial distribution of fish between reef zones, and the population was considered to be at equilibrium (vanRooij et al. 1996b).

Underwater visual censuses were conducted throughout all seasons and times of day, except during crepuscular and spawning periods when the diel migration of fish would have skewed the data spatially. Survey dives were conducted in each of the five reef zones distinguished at Karpata, covering a depth range from 1 to 22 m. In each zone, sampling stations consisted of either six or nine 5 x 5 m plots which were averaged for each zone. Counts were performed 26 times during eight field sampling periods that were separated by approximately three month intervals. Further details of the study site and survey protocols may be found in vanRooij et al. (1996a).

When classified into 50 mm bins, the visual census data exhibit a distinctly bimodal structure (Figure 3.1), highlighting one of the advantages of using *S. viride* as a study animal, namely that all size classes within the population are represented on the reefs, all year round. Juveniles settle directly to the reef (vanRooij et al. 1996a) whereas juveniles of many other species, such as the striped parrotfish, *Scarus iseri*, settle to habitats such as mangroves or seagrass beds (Mumby et al. 2004). For such species, survey data conducted only on the reefs may have a ‘missing mode’ where

the smaller size classes are absent. Furthermore, *S. viride* recruits all year round (vanRooij et al, 1996b), once again ensuring that smaller size classes are included in the data regardless of when the surveys took place. With species that recruit seasonally, smaller fish may be under-represented in census data unless surveys are conducted just after settlement.

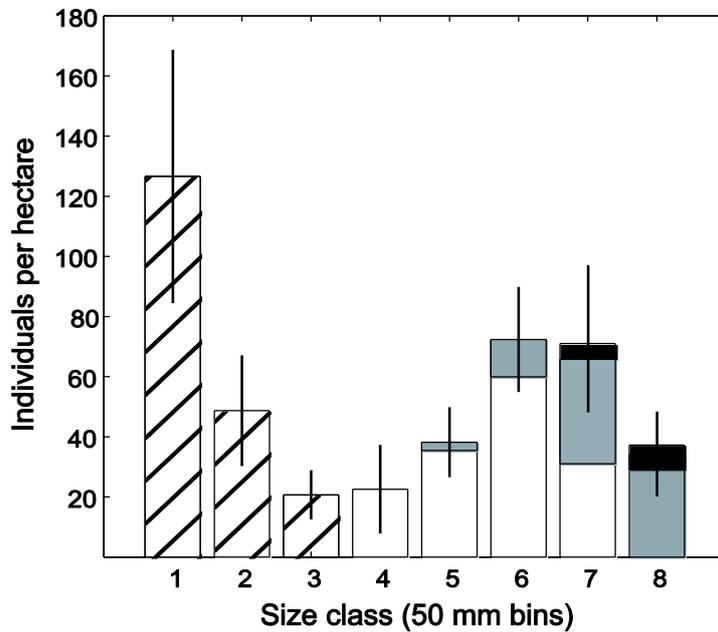


Figure 3.1 Mean size class structure of the *Sparisoma viride* population at Karpata, Bonaire, averaged across all depths and habitats. Diagonal shading represents juveniles, white represents mature females, gray represents bachelor males and black represents territorial males. Error bars show 95% confidence intervals for each class estimated from eight temporally replicated censuses.

In addition to the visual census surveys, somatic growth rates were estimated from mark recapture data, where the body length of tagged individuals was repeatedly measured over time, either directly (vanRooij et al. 1995) or using stereoscopic cameras (vanRooij and Videler 1996). The von Bertalanffy growth function (von Bertalanffy 1934), VBGF, is the most widely used and tested somatic growth equation for fish (Sparre and Venema 1998) and in the present work it is used in the form:

$$L(t) = L_{\infty}(1 - e^{-K(t-t_0)}) \quad (1)$$

where $L(t)$ is the individual's length at time t , L_{∞} is the asymptotic size, e is the base of the natural logarithm, K is the rate at which the curve approaches L_{∞} , and t_0 is the theoretical age when the fish is of zero size (Jennings et al. 1999). L_{∞} and K were estimated for individuals by fitting the VBGF to mark recapture data using nonlinear least squares fitting, resulting in a range of values from which Gaussian distributions (Hart and Chute 2009) of L_{∞} were estimated (Table 3.1). L_{∞} and K are not independent in many fishes but tend rather to be negatively correlated (Pilling et al. 2002). In

the simulations, individuals are randomly assigned an L_{∞} value and a corresponding value for K is then calculated using the coefficients of linear regressions of K on L_{∞} (Table 3.1). Choat et al. (2003) found t_0 to be almost constant between their four study sites, ranging from -0.05 to -0.06, and the median value of -0.055 has been used here.

Summary of Simulation Model

The size structure of a population results largely from the interaction between individual growth and mortality. For example, if fishing introduces novel mortality to populations, commensurate changes may be expected in population size structures (Graham et al. 2005). Such novel mortality may also induce adaptive changes as certain phenotypes become selected for by reaching sexual maturity sooner, enhancing reproductive output before being caught (Enberg et al. 2010). But when growth rates are known for a population experiencing stable mortality, a fair test of a mortality function is how reliably it can approximate the observed size structure. Individual-based simulation models (IBSMs) provide highly flexible tools for exploring such questions, creating virtual populations of individual fish that each have an age and a size (as well as other relevant parameters, such as life-phase), so that population-level mortality patterns emerge from the mortality of individuals, as is the case in nature.

In our simulations, mortality can be applied as any function of individual age or size, separately or simultaneously. The IBSM generates populations of fish through an iterative process whereby individuals are added to the population at an age of one month and a size of 10 mm, representing the arrival of *S. viride* settlers from the plankton (vanRooij et al. 1996a). Individuals then grow and subsequently die, with a high temporal resolution time step of one month,

Growth rates of *S. viride* vary by life phase (vanRooij et al. 1995) so at each monthly iteration fish can change phase once appropriate body size thresholds have been reached (vanRooij et al. 1996b). Phase change occurs probabilistically based on the phase distributions within each 50 mm size class observed in the field data (Figure 3.1).

Younger fish display a unimodal size-at-age structure, whereas older cohorts display bi- or tri-modal distributions, with mean size increasing for mature females, bachelor males and territorial males of the same age (Figure 3.2). This multi-modal size-at-age pattern does not represent the complex size distributions presented in Huston and DeAngelis (1987) which result from intra-population variation in initial size, genes, environment etc. In our modeled population, the variation

in size-at-age arises from the differing reproductive strategies associated with each life phase. Whether further size structure exists within each phase is beyond the scope of the present work.

Quantification of recruitment in coral reef fish is a challenging task (Cowan 2002) and we do not intend the simulations to provide explicit rates of recruitment for *S. viride* in Bonaire. Because the Bonaire population was at equilibrium over the data gathering period, each simulation is allowed to draw in sufficient recruits to replenish losses and maintain population densities near the mean density observed in the field data. Starting from a density of zero individuals per hectare, the simulated population stabilizes after approximately 200 iterations, representing nearly 17 years in real time (Figures 3.4A, 3.4D & 3.4G). The model then runs for a further 100 iterations, with replicate samples being stored every 10 iterations from which mean age and size classes are constructed. After stabilizing, the population density does not deviate substantially from its mean, and we have made no assumptions about post-settlement processes (Hixon and Webster 2002) nor variable replenishment (Doherty 2002) which may contribute to maintaining such densities.

Mortality Functions Tested

The death of each fish is predicted probabilistically within the simulations by applying whichever mortality function is being tested. When age- and size-based mortality are both being applied by the model they act simultaneously but, for clarity, the functions are presented as separate terms in equations 3 and 4 without further simplification. We define and test three functions, namely traditional cohort decay (F_1), size-escape plus cohort decay (F_2), and size-escape plus senescence (F_3).

F₁: Cohort decay (constant mortality)

Cohort decay has been used explicitly to infer population mortality rates in numerous reef fishes, including *S. viride* (Choat et al. 2003, Paddack et al. 2009). In cohort decay mortality, the individual probability of mortality (P_m) at any monthly time step is given by:

$$P_m = 1 - e^{-M/12} \quad (2)$$

where e is the base of the natural logarithm and M is the exponential coefficient of mortality. The function assumes that mortality acts on individuals constantly, causing cohort strength to decay steadily over time.

F₂: Size-escape plus cohort decay (partially trait-dependent mortality)

Predation-induced mortality is commonly higher for juvenile fish, and in the case of *S. viride*, a study of fish size and density along a gradient of predation by grouper concluded that adult fish attained a size-escape from their predators (Mumby et al. 2006). Our second function tested, F_2 , is a modified cohort decay function that allows for elevated mortality in small fish. Cohort decay mortality acts as in F_1 , but there is an additional component that causes size-based mortality to act more intensely on smaller fish, mimicking size-escape from predation by diminishing as the fish grow bigger. We model the size-escape component using the Gompertz function which is a sigmoidal function that was originally developed to model mortality as a function of age in humans (Gompertz, 1825) but has found widespread application since. In F_2 , the combined probability of death at each time step is given by the probability of dying from size-based mortality plus the product of the probabilities of surviving size-based mortality and of dying from cohort decay mortality:

$$P_m = (1 - e^{b \cdot e^{c \cdot L}}) + (e^{b \cdot e^{c \cdot L}})(1 - e^{-M/12}) \quad (3)$$

where e is the base of the natural logarithm, b and c are parameters of the Gompertz function, respectively controlling the horizontal displacement and growth rate of the function, L is the length of the individual and M is the exponential coefficient of mortality. Note that an additional Gompertz parameter is commonly used as a factor to define the upper limit of the function range but is not required here as the limit is 1.

F₃: Size-escape plus senescence (coupled trait-dependent mortality)

Our third and final function couples size-escape from predation with a senescence-like function. Each individual's probability of mortality is negatively influenced by its size, as in F_2 , but here it is also positively influenced by its age. We again use the Gompertz function to model size-based mortality, but we model the age-based component such that the probability of mortality begins to increase exponentially as a function of age after the onset of 'senescence' (Figure 3.5). In F_3 , the combined mortality probability for a fish at any time step is given by the probability of dying from size-based mortality plus the product of the probabilities of surviving size-based mortality and of dying from age-based mortality:

$$P_m = (1 - e^{b \cdot e^{c \cdot L}}) + (e^{b \cdot e^{c \cdot L}})(1 - e^{r \cdot T} / e^s) \quad (4)$$

where e is the base of the natural logarithm, b and c are parameters of the Gompertz function, L is the length of the individual, r is the exponential growth rate, T is the age of the individual, and s is a

scaling parameter that controls the horizontal displacement of the exponential curve, representing the onset of senescence.

Assessing Model Performance

Size Structure

The Karpata population size structure data plotted in Figure 3.1 results from a comprehensive survey campaign covering multiple habitats. Given that the somatic growth rates are also known for the population, we tested the performance of the three mortality functions on how well they can reproduce the observed size classes. Because growth rates and mortality are assigned probabilistically by the IBSM, the equilibrium population fluctuates with each model iteration. To minimize stochastic noise, we sample the simulated population ten times after reaching equilibrium (Figures 3.4A, 3.4D & 3.4G), and we use the resulting mean values to represent each age and size class. To assess fit, we compare the size class frequencies produced by the simulation against the size class frequencies observed in the Bonaire field data. We used a standardized distance (δ) metric whereby the absolute difference between each simulated class frequency and the corresponding observed class frequency is expressed as a proportion of the observed class frequency, and these differences are summed for the eight classes, such that:

$$\delta = \sum_{i=1}^8 \frac{|\bar{\gamma}_i - \bar{\chi}_i|}{\bar{\chi}_i} \quad (5)$$

where δ is the standardized distance between the simulated population and the field data, i represents the size classes, $\bar{\gamma}$ is the mean simulated class frequency, and $\bar{\chi}$ is the mean observed class frequency. We obtain the best fitting parameter values using constrained nonlinear optimization to minimize δ across the parameter space, with initial estimates generated by iteratively randomizing combinations of parameter values.

Individual Longevity

In general, longer lived fishes have slower population turnover times, and thus tend to be more heavily impacted by exploitation. Empirical estimates of longevity were available for *S. viride* from an age-based demographic study (Choat et al. 2003) of populations at four locations across the western Atlantic, namely Barbados, Lee Stocking Island (Bahamas), San Blas (Panama) and Los Roques (Venezuela). Maximum age had been estimated from otoliths (ear stones) which lay down seasonal markings from which the age of the animal can be estimated (Beamish and McFarlane

1983, Campana 2001). The authors found the maximum age to be nine years at all four study sites. The fact that 417 fish were sampled from such a range of habitats, latitudes and fishing pressures lends confidence to the generality of this estimate. The authors state that they considered Los Roques to be very similar to Bonaire in geography, climate and exploitation of *S. viride*, and in the present work, we assess the various models on how accurately they predict this maximum age.

Population Simulations

Simulated populations consist of individual fish, each having age and size characteristics (Figure 3.2), whose growth is determined by the von Bertalanffy growth function, using empirically derived parameters (Table 3.1). Mean estimates of K , the von Bertalanffy growth parameter, for the four life phases range from 0.35 to 0.78, varying from slow-growing territorial males to fast-growing juveniles. At the nearby site of Los Roques, Choat et al. (2003) estimated the overall population average value to be 0.6, which compares favorably. Individuals join the population as month-old females of 10 mm length, and if they survive past empirically-estimated size thresholds they may probabilistically change life phase. When a fish changes phase its growth parameters are reassigned accordingly, as can most clearly be seen in Figure 3.2 for the transition from mature female to bachelor male after ~200 mm, when transitioned males invest heavily in growth at the expense of reproduction, with the hypothesized objective of becoming large enough to achieve territorial status in the future (vanRooy et al. 1995).

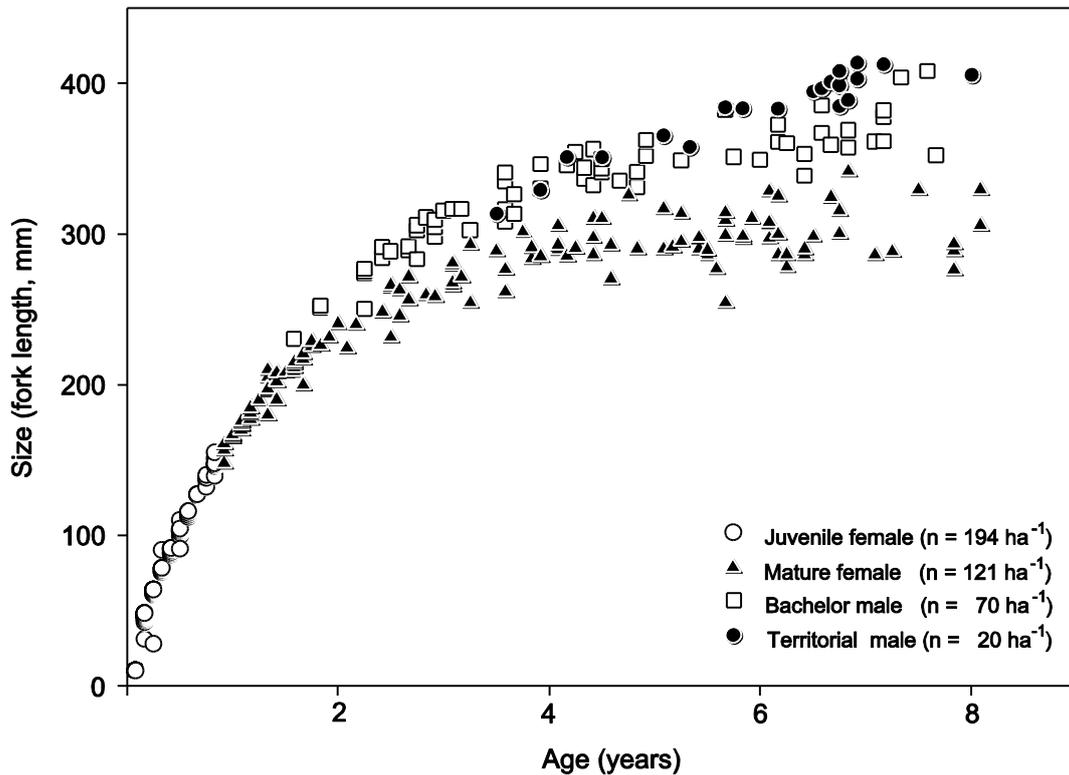


Figure 3.2 Typical life phase composition and size-at-age of individuals in a simulated population of *Sparisoma viride*. Symbols indicate the ontogenetic and/or social status of individuals, representing the population demographic structure averaged across all habitats from 1 to 22 m depth. Age was converted to length using the parameters of the von Bertalanffy growth function estimated from empirical mark recapture data (Table 3.1) at the study site. Residuals follow a Gaussian distribution around the mean growth trajectory for each phase. Individuals may probabilistically change phase, following empirical proportions of phases recorded in each size class at Karpata (Figure 3.1). When individuals change phase their growth parameters are reassigned accordingly. The simulation used to produce the illustrated population was F₃, which incorporated coupled size-escape and senescence mortality.

Table 3.1 Parameter values for the von Bertalanffy growth function estimated from mark recapture field data, and used to calculate size-at-age by life phase in the simulation model.

Life phase	L_{∞}	K	mean K
Juvenile female	293 +- 31	$K = 1.869 - 0.0037 L_{\infty}$	0.78
Mature female	305 +- 16	$K = 1.901 - 0.004 L_{\infty}$	0.68
Bachelor male	388 +- 21	$K = 1.2458 - 0.0018 L_{\infty}$	0.55
Territorial male	438 +- 19	$K = 1.0546 - 0.0016 L_{\infty}$	0.35

L_{∞} : Mean asymptotic lengths (mm) +- SD.

K : Intercepts and slopes of linear regressions on L_{∞}

mean K : value of K for the mean L_{∞} of each phase

Results

Empirical Testing of Simulated Populations

F₁: Cohort decay (constant mortality)

The parameters of the individual-based simulation model (IBSM) fitted with the cohort decay mortality function (F_1) were: density of settlers per month, ‘Settlers’, and the coefficient of natural mortality, M . Respectively, the optimized values were 6 and 0.26 which produce a model fit with a standardized distance of 2.818 (Figure 3.3). The resulting simulated population stabilizes at densities considerably below those observed in the field (Figure 3.4A). The population decays exponentially with age, as expected from cohort decay mortality, predicting a maximum age of 16 years (Figure 3.4B). In the size-classified data (Figure 3.4C), six out of the eight size classes produced are within the 95% confidence intervals of the field data, showing that cohort decay mortality performs reasonably well at simulating the larger classes. However, the two smallest classes are substantially underestimated, creating the population deficit apparent in Figure 3.4A.

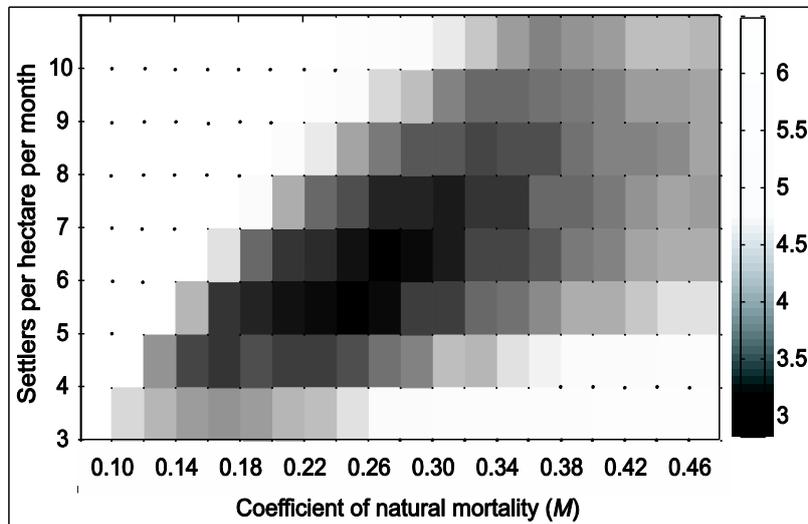


Figure 3.3 Surface plot of the fits produced from a range of parameter sets by the IBSM incorporating cohort decay mortality, F_1 . The scale bar on the right represents standardized distance, which is a measure of difference between the simulated data and the field data, smaller values indicating a better fit. The best fit to the data was obtained for the combination $M = 0.26$ and Settlers = 6. As the parameter combinations get further from the optimal solution, the standardized distance between the model output and the field data increases. The diagonal trend of the fits from the bottom left to the top right of the plot is created by a trade-off, where higher rates of mortality are partially compensated for by higher rates of settlement.

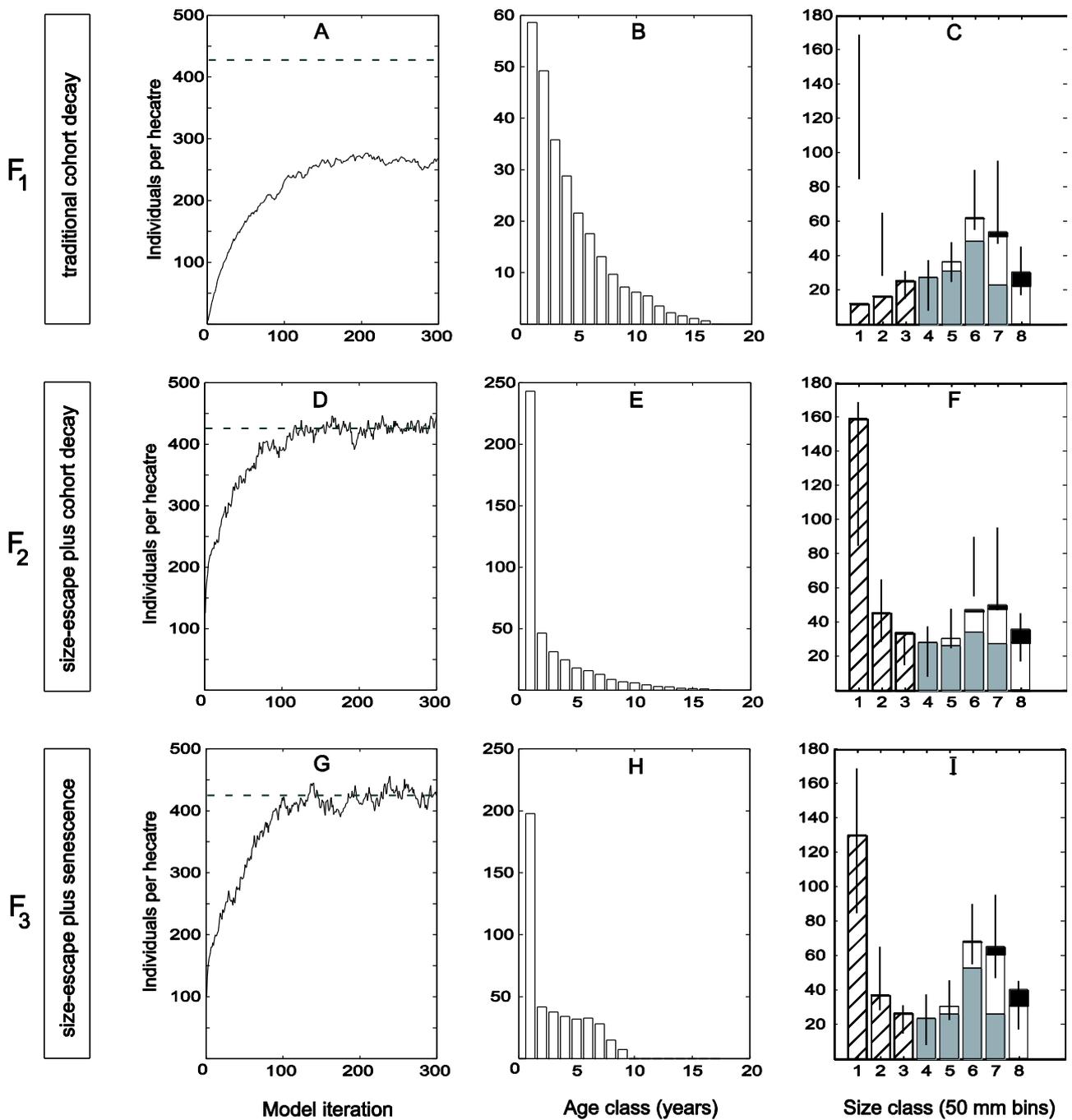


Figure 3.4 Summarised outputs of individual-based simulation model incorporating three different mortality functions, plotted top to bottom, and parameterized with values optimized against field data. Panels in left-hand column represent population density per model iteration, and the dashed lines indicate the mean population density of the field data. Middle column shows the simulated population age structure in year classes (cohorts). Note that the vertical scale varies. Right-hand column shows the simulated population size structure classified into 50 mm bins, and error bars show 95% confidence intervals of field data. Diagonal shading represents juveniles, white represents mature females, gray represents bachelor males and black represents territorial males. To minimize the stochastic variation that can be seen in the left-hand panels, the age- and size-class plots represent values averaged from ten samples taken from the simulated population after equilibrium was achieved.

F₂: Size-escape plus cohort decay (partially trait-dependent mortality)

The second mortality function couples two components: a constant that causes cohorts to decay exponentially and a size-based function that negatively influences the mortality probability as a fish grows bigger towards an escape size (equation 3). The parameters optimized for the second mortality function (with values in parentheses) were: Settlers (125), M (0.28), and the Gompertz parameters, b (-1.61) and c (-0.024). Parameterising the F_2 model with these values produces the population illustrated in the second row of Figure 3.4. It can be seen from Figure 3.4D that the population stabilizes around the mean empirical population density. As with the first model tested, F_1 , the maximum predicted age is 16 years, as shown in Figure 3.4E. F_2 also simulates six out of the eight size classes to within the 95% confidence intervals of the field data (Figure 3.4F), with a standardized distance of 1.98.

F₃: Size-escape plus senescence (coupled trait-dependent mortality)

The third and final mortality function has two components (equation 4). The size-based component in F_3 once again represents size-escape from predation, but here the age-based component mimics senescence. The optimized parameters (with values in parentheses) were: Settlers (98), the Gompertz parameters b (-1.45) and c (-0.021) which model size-escape, and two parameters, r (0.14) and s (15), of an exponential function that models senescence. The optimized size- and age-based functions are plotted separately in Figure 3.5, illustrating how the size-escape function negatively influences the probability of mortality as a fish grows towards an escape size, while the senescence-like function positively influences the probability of mortality as a fish becomes older.

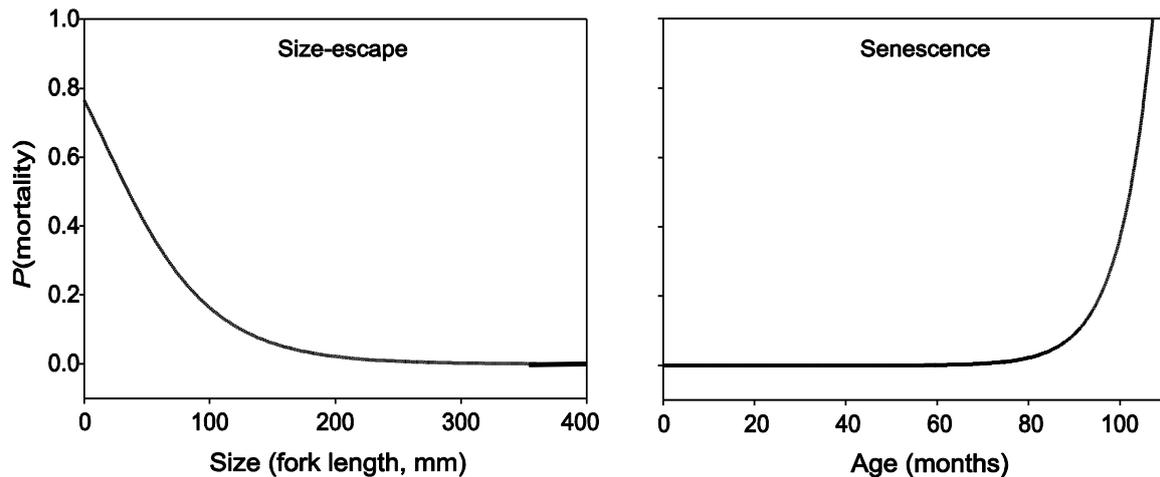


Figure 3.5 Graphic representation of the trait-dependent functions coupled in simulation F_3 to calculate the probability of mortality for an individual fish as a function of its size (left) and age (right), which are the right-hand terms in equation (4). Functions are plotted using the parameter values optimized in simulation F_3 .

The bottom row of plots in Figure 3.4 shows the summary outputs of the F_3 model parameterized with the optimal values. As with F_2 , the population comfortably stabilizes around the mean empirical density (Figure 3.4G). However, F_3 produces an improved fit to the empirical size class data (Figure 3.4I), where all eight simulated classes are within the confidence intervals of the field data, with a standardized distance of 0.95. A more striking difference between F_2 and F_3 , however, is in the age structure. Where F_2 predicts longevity at 16 years, F_3 predicts a maximum age of only 9 years (Figure 3.4H).

Discussion

Model Performance: Simulations of Size Data

The optimized value for the cohort decay parameter, M , used in simulation F_1 was 0.26 which compares very favorably with the empirical estimate of 0.24 obtained by Choat et al. (2003) for their study population at Los Roques. However, despite such agreement with an empirical parameter estimate, and the reliability of the growth rates used in our simulations, the cohort decay function performed poorly at replicating our empirical size structure data (Figure 3.4C), predicting densities of the smaller size classes that were considerably lower than those observed.

Considering that the F_1 simulation reaches equilibrium far below the field data, and that the optimized number of settlers ($n = 6$) is also low relative to simulations F_2 and F_3 ($n = 125$ and 98

respectively), it is tempting to wonder if the fit may be improved by increasing the number of settlers while simultaneously increasing mortality to retain the fit in the larger classes. That this action would not improve the fit illustrates one of the drawbacks of the cohort decay function. As growth rate slows with age, fish tend to spend more time in successively larger size classes and adding more settlers to the each smaller size class tends to induce an accumulation of fish in the next. The only way to overcome this tendency is to greatly increase mortality, and indeed it would be expected that such small fish would experience very high mortality. However, cohort decay assumes that mortality acts equally on all individuals and so as M increases, mortality also increases for older fish, and the probability of any individual surviving long enough to reach the larger classes becomes vanishingly small.

As expected, the incorporation of the size-escape component in simulation F_2 improved model performance over simulation F_1 in the juvenile classes, and with simulated densities for the two smallest classes now settling within the 95% confidence intervals of the field data. Simulation F_3 considerably outperformed both of the others, however, replicating the densities in all eight size classes to within the statistical bounds.

Model Performance: Simulations of Age Data

The maximum longevity predicted by both of the simulations that incorporate the cohort decay function, F_1 and F_2 , was 16 years (Figures 3.4B and 3.4E), but the prediction of the fully trait-dependent simulation, F_3 , was only nine years. The 2003 study by Choat et al. provides two lines of evidence that support the fully trait-dependent model, namely the maximum longevity itself and the way in which the data approach that maximum. From a sample size of 417 *S. viride*, Choat et al. (2003) also found the maximum age consistently to be nine years at all four of their study sites, which represented a wide range of latitudes and fishing intensities, matching the prediction of F_3 .

In both of the cohort decay simulations mortality remains constant for older fish and so age classes decrease steadily towards the maxima (Figures 3.4B and 3.4E). In the F_3 simulation, mortality changes non-linearly as fish grow older, resulting in an abrupt decrease in the age-frequency data as the maximum longevity is approached (Figure 3.4H). A similarly abrupt change is also evident in the Los Roques field data from Choat et al. (2003) (Figure 3.6). The study examined the otoliths from 118 individuals at the site which represented the only unexploited population in their study.

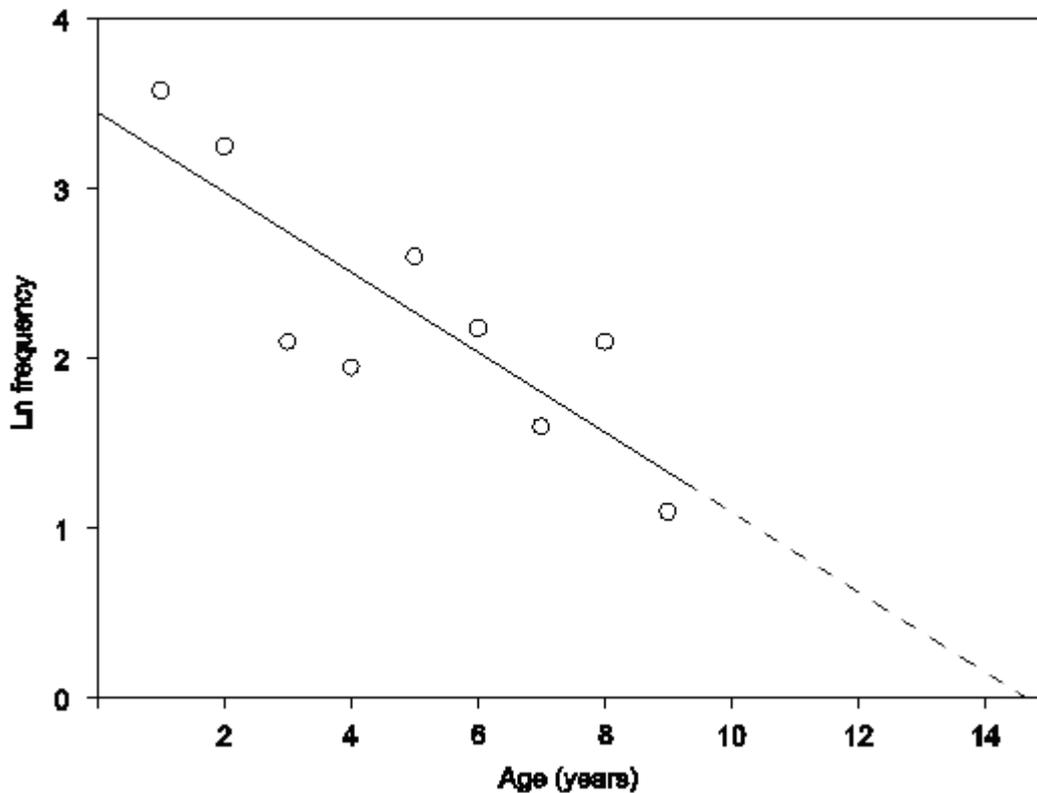


Figure 3.6. Empirical age frequency data of the *Sparisoma viride* population at Los Roques, Venezuela, reproduced from Choat et al. (2003). Markers represent the natural logarithm of the mean number of individuals sampled from each age class, as estimated from otolith reading. The solid portion of the line represents the best fit to the data (equation 6) as assessed by Choat et al. (2003), the slope of which estimates the coefficient of natural mortality, M . The dashed portion of the line represents the fit when it is extended to the x-intercept, when frequency of observation reaches zero.

Choat et al. (2003) implicitly assumed that mortality was constant for the population by fitting the cohort decay function, represented by the line of best fit plotted in Figure 3.6 and given by the equation:

$$\ln(y) = -0.24 x + 3.46 \quad (6)$$

where y is the year class frequency, and x is age. The slope of the line, -0.24 , is the estimate of M for the population. Choat et al. (2003) do not extend the line to the horizontal intercept, as we have done here, but maximum age is predicted by a linear function where the age frequency reaches zero. Solving equation (6) for $y = 0$ predicts a maximum age of 14.4 years, yet as can be seen from the plot, no fish that were even close to this age were observed in the field. While it is possible that such fish do exist but were not included in the sample, this explanation seems unlikely given the generous sample size. The parsimonious alternative is that *S. viride* at Los Roques do not live for

nearly as long as cohort decay mortality predicts, and the abrupt ‘disappearance’ of the cohort after nine years signals a change in the way mortality acts on the population, such as the onset of senescence.

A further line of evidence supporting the fully trait-dependent model, F_3 , is found in Mumby et al. (2006). In a study of trophic cascades in the Exuma Cays Land and Sea Park (ECLSP), Bahamas, the authors found that *S. viride* did indeed experience a size-escape when they became too large for the gape of the most common predators. The F_3 simulation in the present work predicts that escape is reached at a slightly smaller size in Bonaire (Figure 3.5), which is to be expected given that large predators are considerably less abundant in Bonaire than in the ECLSP.

The Evolution of Senescence in Parrotfishes

Our best fitting model assumes that the study population experiences senescence, here applied in a simplistic manner despite the inherent complexities of the phenomenon. The significance of senescence has been debated for more than half a century, with early theories centered on the notion that aging existed simply as an epiphenomenon of selection. Broadly speaking, theories of aging can be classified into two schools of thought, ‘mutation accumulation’ and ‘antagonistic pleiotropy’ (Abrams and Ludwig 1995, Reznick et al. 2004). Mutation accumulation holds that senescence results from the accumulation of deleterious mutations whose effects are manifest only in post-reproductive individuals, thereby making them invisible to selection (Medawar 1952). Conversely, antagonistic pleiotropy contends that certain genetic traits may induce vigor in pre/reproductive life stages at the expense of post-reproductive stages, so that although senescence arises from adaptive processes it is not in itself selected for (Williams 1957). It is not currently known whether *S. viride* ever become post-reproductive, but changes in the action of aging may be linked to abrupt changes in reproductive investment commensurate with social status.

A variant of antagonistic pleiotropy called the ‘disposable soma’ theory propounds that elevated senescence following the commencement of reproduction is caused by a diversion of energy resources that would otherwise be used for somatic repair (Kirkwood and Cremer 1982, Abrams and Ludwig 1995). There can be few fishes which invest as heavily in reproduction as territorial male *S. viride*, which mate daily with multiple partners, all year round, and the existence of elevated senescence under such circumstances may be hypothesized, especially given the low nutritional density of the species’ food resources (Bruggemann et al. 1994).

It has been shown in disparate organisms that mortality rates increase until late in life and then begins to decrease again (Carey et al. 1992, Curtsinger et al. 1992, Reznick and Ghalambor 1999). We found that modeling mortality as a continuous exponential function of age provided good fits to the field data, but this should not necessarily be interpreted as the absence of a late life mortality plateau. We fitted a single mortality function to all three adult life phases, as to employ three separate mortality functions would be to risk considerable over-fitting, but the very different reproductive outputs of the three adult life phases suggest that mortality may, in actuality, vary considerably between the three. Indeed, the social organization of *S. viride* may lend itself well to testing the disposable soma theory in coral reef fish. In *S. viride* populations, the overwhelming majority of mating involves territorial males, which were observed to spawn an average of six times a day at Karpata, up to a maximum of 13 times (vanRooij et al. 1996b). When a territorial male dies it is replaced by a bachelor male that has forgone reproduction until that point. Under the disposable soma theory it may be expected that bachelor and territorial males of the same age may experience quite different levels of senescence.

Conclusions

Many small-bodied fishes may never grow large enough to achieve a size-escape from predators, and losses from the population may be more or less random, and thus adequately modeled by cohort decay. The approach may also work well for many traditional stocks that recruit at an early age when juveniles join large aggregations of adults, thereby enjoying an early-stage release from predation. But for many larger-bodied species that achieve a size-escape later in life, including macro-predators which are commonly preyed upon as juveniles, mortality may change profoundly during the course of their lives. For such species, the cohort decay function will perform poorly.

An additional benefit of our coupled simulation approach is that it provides the opportunity to gauge how changes to mortality may affect a population, with the advantage of allowing the intrinsic and extrinsic components of mortality to be varied independently. For example, intrinsic mortality may be unaffected by the arrival of a novel predator in the short to medium term, but intensification of extrinsic mortality may be rapid, as is the case in the invasion of western Atlantic reefs by Indo Pacific lionfish, *Pterois* spp., that is currently underway (Côté and Maljković 2010).

By incorporating trait-dependent functions that explicitly represent the mortality processes underlying a population, our best simulation succeeded well in replicating field data without

requiring the sacrifice of large numbers of fish, an unfortunate requirement of many traditional approaches which rely on otolith data. As an increasing number of species becomes endangered and/or over-exploited, the capacity to explore complex age and size structures of populations without further damaging those populations is becoming increasingly valuable, and individual-based simulations represent powerful and flexible tools in the study and management of wildlife.

Acknowledgements

The authors wish to extend their sincere thanks to Graham Pilling for valuable contributions and criticisms and to the UK Natural Environment Research Council and Cefas for project funding.

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4

Estimation by elimination: A simple least squares method for approximating von Bertalanffy growth parameters from tagging data

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Abstract

Population models are fundamental to assessing many impacts of natural or anthropogenic disturbances on fish stocks, and the utility of such models is contingent upon accuracy in estimation of somatic growth rates. Traditionally, growth parameters were estimated using size-at-age data obtained from lethally-sampled otoliths (ear stones). However, such methods are inappropriate for vulnerable or ecologically-important species, and much interest has been shown in finding non-lethal alternatives, such as parameter estimation from tagging data. We present a novel solution to the problem that exploits the disproportionately large response of asymptotic length (L_{∞}) to a small misestimate of true age during fitting of the von Bertalanffy Growth function (VBGF). Using simulated data, we find that our method performs better than the most commonly used approach, Fabens' method, especially for small sample sizes where our method produces estimates of the VBGF parameters, L_{∞} and K , that are respectively 66% and 35% more accurate. Our method shows promise for coral reef fish studies, where recapture rates in tagging studies are typically very low yet the lethal sampling of fishes is often undesirable.

Keywords: von Bertalanffy, Fabens, mark recapture, tagging, growth estimation, stock assessment

Introduction

The growth characteristics of animals are linked intrinsically to their life histories. For example, larger bodied species tend to produce fewer offspring, longer lived animals tend to grow larger (Speakman 2005) and animals that grow faster as juveniles tend to end up smaller as adults (Atkinson and Sibly 1997). Because it is often more tractable to estimate parameters at the level of individuals rather than populations, much interest has been shown in determining which, if any, individual characteristics provide the most robust inferences about populations (Pauly 1980).

Although many functions have been used to model somatic growth in fishes (Schnute 1981, Laslett et al. 2002), the von Bertalanffy growth function (VBGF) is the most widely used equation in fisheries science (Ricker 1979, Francis 1988, Laslett et al. 2002) and the parameters of the VBGF (von Bertalanffy 1934) have long been used make inferences about the ecology and life history of fish populations (see, for example, Beverton and Holt 1957). In its general form, the VBGF expresses size (length or weight) L at age t such that:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \quad (1)$$

where L_∞ is the asymptotic size, e is the base of the natural logarithm, K is the rate at which the curve approaches L_∞ , and t_0 is the theoretical age when the fish is of zero size (Jennings et al. 1999). The parameters are commonly estimated by fitting the VBGF to size-at-age data, where the age of each fish is estimated from the relationship between otolith (ear stone) weight and fish age (Lou et al. 2005) or more commonly from enumeration of incremental markings (*annuli*, Latin: ‘rings’) on hard body parts including otoliths, bones and scales (Beamish and Chilton 1977, Campana 2001). Various factors can cause material to be laid down in such a pattern, such as disease and reallocation of resources during periods of reproduction (Baltz 1990), but the annuli are commonly laid down through the physiological response of fish to seasonal variation in water temperature. Such is the prevalence of age-based approaches that between one and two million fish are aged each year by researchers (Campana and Thorrold 2001).

Although otolith reading has proven its usefulness time and again for many populations, a number of drawbacks to this approach remain. The generation of useful data from otoliths requires skilled visual interpretation of banding by multiple readers (Campana 2001), following a period of laborious mounting, grinding and polishing of the otoliths. Otolith reading requires a large sample size which, in commercial fisheries, can readily be obtained from landings, but the sacrifice of large numbers of fish limits the usefulness of the technique in vulnerable, protected, or ecologically

important species. Furthermore, it is vital that the periodicity of annuli be validated from each new stock assessed but doing so is time-consuming and logistically challenging and this requirement is frequently ignored (Beamish and McFarlane 1983) casting some doubt on the validity of some of the data collected.

An alternative approach for estimating growth parameters is to use mark-release-recapture (MRR) data, where individuals are measured, tagged and released, and then subsequently recaptured after a known time period and re-measured. Fabens' (1965) approach is the most widely used method for estimating the parameters of the VBGF from tagging data (Laslett et al. 2002) where the size at time of capture, L_t , and at recapture, L_{t+1} , can each be expressed in the form of eqn. 1, producing a pair of equations that can be solved through substitution, and then rearranged so that the size at recapture is expressed as:

$$L_{t+1} = L_t + (L_\infty - L_t)(1 - e^{-Kd}) \quad (2)$$

where d is time elapsed between the measurements. Tagging data provide a range of paired values for the dependent and independent variables, L_{t+1} and L_t , and eqn. 2 can be fitted to these data to produce estimates for asymptotic length, L_∞ , and the growth coefficient, K . The fitting method used is nonlinear least squares (NLS) which is the most widely used and understood nonlinear fitting procedure, probably contributing to the ongoing popularity of the method.

A limitation of the approach, however, is that it does not account for individual variability in growth which can induce bias in the fitted parameters (Eveson et al. 2007). A number of more sophisticated methods have been developed that can accommodate such variability, but many require the user to be fluent in, *inter alia*, Bayesian hierarchical models (e.g., Zhang et al. 2009), mixed effects models (e.g., Hart and Chute 2009) or maximum likelihood models (e.g., Laslett et al. 2002) which are not as widely understood as NLS. Some simpler regression-based methods have also been developed but these generally do not handle individual variability much better than Fabens method (Smith et al. 1997).

Here we present and test a novel method for parameter estimation that uses simple NLS fitting, and we compare its performance against that of Fabens' method, using simulated populations of fish which display individual variability in growth. Our method requires the user to supply a broad 'guesstimate' of a range within which they estimate where the true population L_∞ plausibly lies. An appropriate range may be estimated for many species from the size of individuals within the population (Pauly 1980). We test our method using five scenarios wherein we vary the accuracy in the user-supplied range of plausible values and we find that the method can produce very good

estimates of true L_{∞} and K but that it is sensitive to error in the plausible range that is assumed. However, we find that accuracy may be assessed from the outputs themselves and the most likely parameter values may thus be selected from the series of scenarios, and that the resulting estimates are considerably better than those of the Fabens method, especially at low levels of replication.

Methods

Description of procedure

The VBGF captures the nonlinear relationship between size and age in fishes. With tagging data, the size at capture and recapture are known, as is the time lag between the measurements. It is also known that at zero age, the fish was more or less of zero size. What is not known is the absolute age of the fish at either time. In the context of a size-at-age plot, these unknown ages correspond to the unknown displacement of the couplet of measurements along the horizontal axis. When the VBGF curve is fitted to data and forced through the origin, a relatively small error in this horizontal displacement induces a disproportionately large change in the curve when it is projected to infinity, as modelled by the asymptotic size parameter, L_{∞} . If we can make very broad estimates of the true values of L_{∞} and K , we can usually eliminate the displacements that are implausible. An approximate value of mean L_{∞} for a population may usually be estimated from the size distribution. For relatively small bodied fish species such as the one used in this example, the true population value of L_{∞} is generally close to the observed maximum size of the fish in the population and empirical ratios are available for larger bodied species (Pauly 1980).

To illustrate, we use a hypothetical fish with a true $L_{\infty} = 300$ mm, $K = 0.5$ and $t_0 = 0.055$. If captured at the age of two years and then recaptured at three years, its size measurements would be 186 mm and 231 mm respectively (from eqn.1), shown as the couplet of black squares in Figure 4.1a. In reality, we would not know the true horizontal displacement, so we iteratively displace the couplet along the horizontal axis, illustrated at four positions in Figure 4.1a, labelled *a-d*. To test the robustness of the technique, we ensure that the candidate displacements do not precisely match the true displacement. We then fit the VBGF through the couplet at each displacement and through the origin, as plotted in Figure 4.1b. The fitted parameters are reported in Table 4.1.

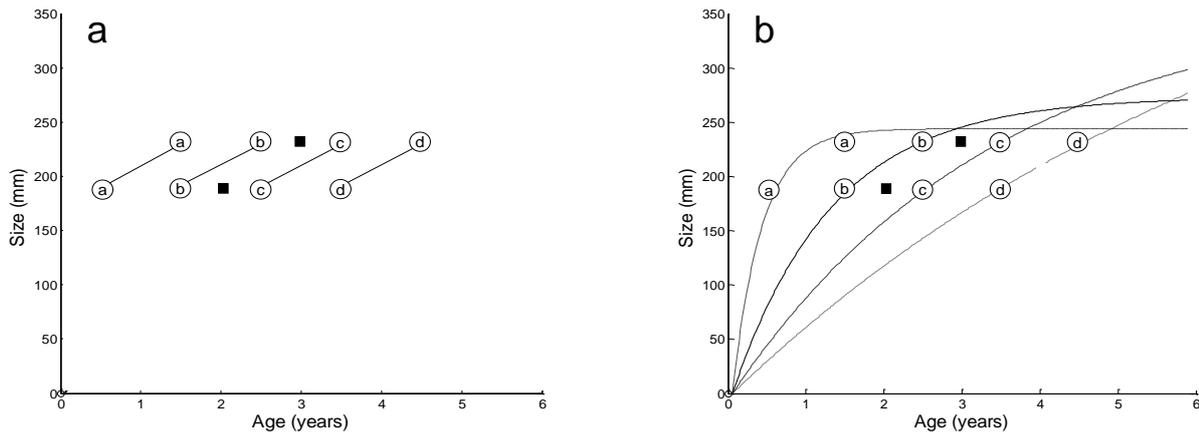


Figure 4.1 Conceptual diagram of the parameter estimation process using a model fish with an arbitrary asymptotic length, L_{∞} , of 300 mm, a growth coefficient, K , of 0.5 and a theoretical age at size zero, t_0 , of 0.055. These parameter values are used to produce a couplet of size measurements when the fish is 2 and 3 years of age, representing age at first capture and age at recapture and marked with black squares in both panels. The displacements $a-d$ (panel a) are candidate positions whose plausibility is assessed by fitting the von Bertalanffy growth function (lines, panel b) to each displacement and through the origin, and then eliminating the displacements that produce implausible parameter fits (Table 4.1).

Table 4.1 Parameter estimates produced from fitting the von Bertalanffy growth function to incremental horizontal displacements of a couplet of size measurements taken at a known time interval, in this case one year.

Displacement	Fitted L_{∞}	Fitted K
<i>A</i>	244	2.62
<i>B</i>	273	0.77
<i>C</i>	365	0.29
<i>D</i>	721	0.09

From the fitted values shown in Table 4.1, we eliminate displacement a for having an implausibly high value for K (2.62), and we eliminate displacement d (and any subsequent displacements) as being far outside a plausible range of values for L_{∞} (721 mm). Although displacement c produced a very high fitted L_{∞} (365 mm), if our knowledge of the actual population size structure does not allow us to confidently eliminate the estimate as being impossibly large, we should retain it. Then using the fitted parameters of the non-eliminated displacements, here $L_{\infty} = (273, 365)$ and $K = (0.77, 0.29)$, we calculate the geometric means of those parameters, giving us estimates of 316 mm and 0.47. These constitute replicate estimates for that fish and although they compare reasonably well with the true values (300 mm and 0.5) it should be stressed that the procedure is not intended to provide reliable estimates for any individual fish, but rather to provide a series of replicates which will be distributed randomly around the true population parameters.

We then go on to conduct the same procedure for each fish in our sample, and the overall mean for each parameter represents the population estimate. We use geometric means to dampen the effects of extreme fits, but if only one displacement produces plausible fits, we simply use those values. It is worth stressing that these estimates were produced from a ‘worst-case’ scenario, when none of the candidate displacements was within six months of the true displacement (Figure 4.1a).

The illustrated example shows that our simple method produces reasonable parameter estimates for an individual fish. Next we test the method by applying it to simulated populations of fish in which the growth parameters are allowed to vary among individuals, and we compare the performance of our method (hereafter, the ‘elimination method’) to that of Fabens to determine which one better accommodates individual variability, at varying levels of replication.

Simulations

The values used in the simulations are not intended to represent any species in particular, but simply to provide a convenient yet credible parameter space. Within the simulated population, the values of L_{∞} for individuals is assumed to approximate a normal distribution which is intuitively likely and not rejected by empirical data (Laslett et al. 2002). The mean population value for L_{∞} is set at 300 mm, with a standard deviation of 20 mm, meaning that 95% of individuals in the simulated populations will have an L_{∞} of between 260 and 340 mm.

The relationship between L_{∞} and K is assumed to be negatively linear (Francis 1988, Pilling et al. 2002), and the slope of the line used in the present work to parameterise the relationship was that empirically estimated by O’Farrell et al. (2011) for small (up to ~300mm) Caribbean stoplight parrotfish (*Sparisoma viride*), namely $-0.0037 L_{\infty}$. The intercept has been adjusted to produce an arbitrary but convenient mean K value of 0.5, given by:

$$K = 1.61 - 0.0037L_{\infty} \quad (3)$$

In addition to L_{∞} and K , the classical VBGF contains an estimate of the theoretical age (t_0) of a fish when its size is zero. Here, we used the value of -0.055 years, which is the mean empirical estimate produced by Choat et al. (2003) in a study of *S. viride*.

The size range of fish sampled in the simulations is restricted to between 100 mm and 250 mm. Individuals smaller than 100 mm were omitted because many fishes experience very high levels of

juvenile mortality (Dahlgren and Eggleston 2000, Almany and Webster 2006, Craig et al. 2006) and tagging very young individuals in the wild may result in a very low rate of recapture. Conversely, large fish that are approaching their asymptotic size will grow very little between capture and recapture, and the lack of variation in the response variable (size) will provide restricted information for the analysis.

Fabens' methods and the elimination method are both tested by iteratively simulating 100 'populations' of fish, whose growth parameters vary individually round the population mean. These are not true model populations that have been parameterised with rates of recruitment and mortality, but are simply collections of fish whose growth parameters vary as described, which is adequate for our purposes. For each population, the methods are passed sets of replicates, sequentially increasing in number from two to 30. For each n replicates, the methods estimate the population parameters. After the 100 simulated populations have been assessed, the stored values are converted to the mean ($n = 100$) parameter values for each n (2:30) replicates. For the plots, these are expressed as the distance (absolute difference) between the estimated value and the true value.

This fitting procedure is straightforward for testing Fabens' method, but to test the elimination method the program must make 'decisions' as to whether the fitted values produced by a given displacement are plausible or not, as the 'user' did in the example. We test five scenarios in which the plausible range varies. All five ranges are 100 mm wide and contain the true L_∞ of 300 mm, but we incrementally shift the range around the position of true L_∞ (Table 4.2). Lying in the middle of the five, scenario 3 represents a perfect estimate, where true L_∞ is located in the centre of the plausible range (250 – 350 mm). Scenarios 1 and 2 represent varying degrees of underestimation and scenarios 4 and 5 are varying degrees of overestimation.

Table 4.2 Ranges of L_∞ used by the elimination method simulations to assess whether the fitted values of L_∞ returned for a given horizontal displacement are considered plausible.

Scenario	Plausible range	Midpoint
1 Extreme underestimate	210 – 310 mm	260
2 Moderate underestimate	230 – 330 mm	280
3 Correct estimate	250 – 350 mm	300
4 Moderate overestimate	270 – 370 mm	320
5 Extreme overestimate	290 – 390 mm	340

We fix the maximum acceptable value of K at 1.5, which would be an implausibly high value for a fish of the size range we are simulating. For example, Choat et al. (2003) estimated VBGF parameters for *S. viride* at four locations across the wider Caribbean. The values of L_∞ estimated in the study ranged from 264 mm to 357 mm, which are similar to the likely ranges produced by our simulations, and the estimates of K ranged from 0.45 to 0.82.

The candidate horizontal displacements in simulations (illustrated in Figure 4.1a, positions *a-d*) are spaced at one year intervals, as is usual in otolith-reading analyses which generally attempt to estimate age to within one year. If our simulated fish were assumed to recruit annually, their ages (and thus true horizontal displacements) would also have a temporal resolution of one year, making the parameter estimation easier for the elimination method as one of the candidate displacements would always synchronise perfectly with that the ‘true’ displacement of the fish on the age axis. To challenge the method more thoroughly and to make the test more general, we give the simulated fish a temporal resolution of one month, representing fishes that recruit all year round, such as many coral reef species. This means that there is only a 1 in 12 chance of the candidate displacement aligning perfectly with the true displacement, adding random noise to the data and making the task more difficult for the elimination method.

Results

By allowing individual values of L_∞ to be sampled from the normal distribution and coupling K as a negative linear function of L_∞ , a wide range of individual growth trajectories could be generated (Figure 4.2). The plotted parameter space displays increasing divergence of size with age, as is commonly observed in empirical fish data (Francis 1988, Grist et al. 2011). Individuals selected for use in the analysis were restricted to those with body sizes between 100 and 250 mm, and not all of the size-at-age coordinates plotted in Figure 4.2 will have been assessed.

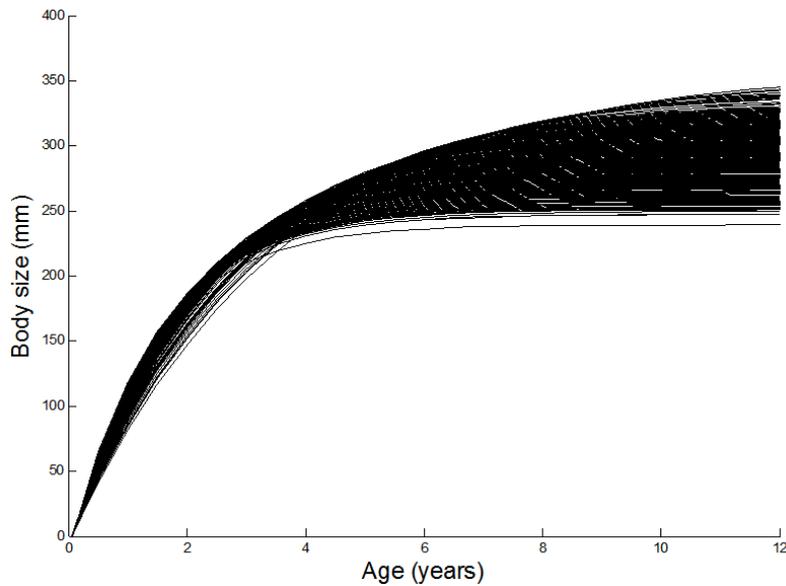


Figure 4.2 The size-at-age parameter space represented in the simulations, where mean $L_{\infty} = 300$ mm (± 20 mm s.d.) and mean $K = 0.5$. For each individual simulated fish, L_{∞} is assigned probabilistically and K is then calculated as a linear function of L_{∞} . In the simulations, fish smaller than 100 mm or larger than 250 mm were disregarded for pragmatic purposes, as discussed in the text.

After imposing the size limits, a substantial range of ages remained in the data subset used during the analysis, as typified by the histogram of frequency and the fitted probability density function of age occurrence (Figure 4.3).

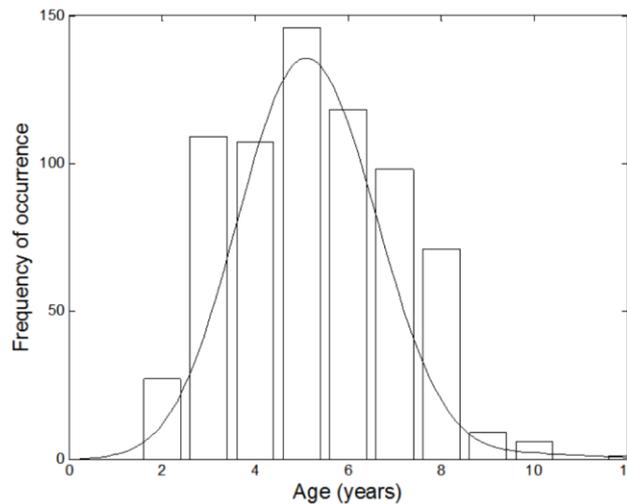


Figure 4.3 Age frequency and probability density function of the ages represented in a sample dataset after it has been subsetted to contain only fish between 100 and 250 mm FL.

For both Fabens' method and the elimination method, the accuracy of the estimates of K (Figures 4.4a and 4.4b) generally improves with the number of replicates included in the estimation. As expected, the two extreme scenarios (1, extreme underestimate; 5, extreme overestimate) of the elimination method perform very poorly (Figure 4.4b), and neither improves substantially with

replication. Scenario 3 (correct estimate) and scenario 4 (moderate overestimate) both do well even at low levels of replication, the former estimating K to within 10% of its true value with only three replicates on average, and the latter with seven replicates on average.

When estimating values of L_{∞} , Fabens' method (Figure 4.4c) again performs very poorly at low replication but settles rapidly, and with only 10 replicates it produces fitted values of L_{∞} that are within 10 mm of the true value. The extreme scenarios (1 and 5) of the elimination method again perform poorly (Figure 4.4d) but scenarios 2,3 and 4 all perform considerably better than Fabens' method at low level of replication, each requiring fewer than five replicates to produce fitted values that are within 10 mm of the true value.

That the elimination method is less accurate when it is supplied with a less accurate plausible range for L_{∞} is not surprising. However, an interesting and useful property of the method is that regardless of the inaccuracy of the plausible range, the fitted L_{∞} values tend towards the true value. When the plausible range is an underestimate, as in scenarios 1 and 2, the distributions of fitted values are not centred within their respective ranges but are up-shifted upwards towards the true value (Figure 4.5, dashed line), and down-shifted within the range when the plausible range is overestimated in scenarios 4 and 5. From this finding, we can assess which plausible range was the best estimate: in the present example, we can see that scenario 3 has the most centrally-placed distribution within its own range, and we should thus select the parameter values estimated during the fitting of that scenario.

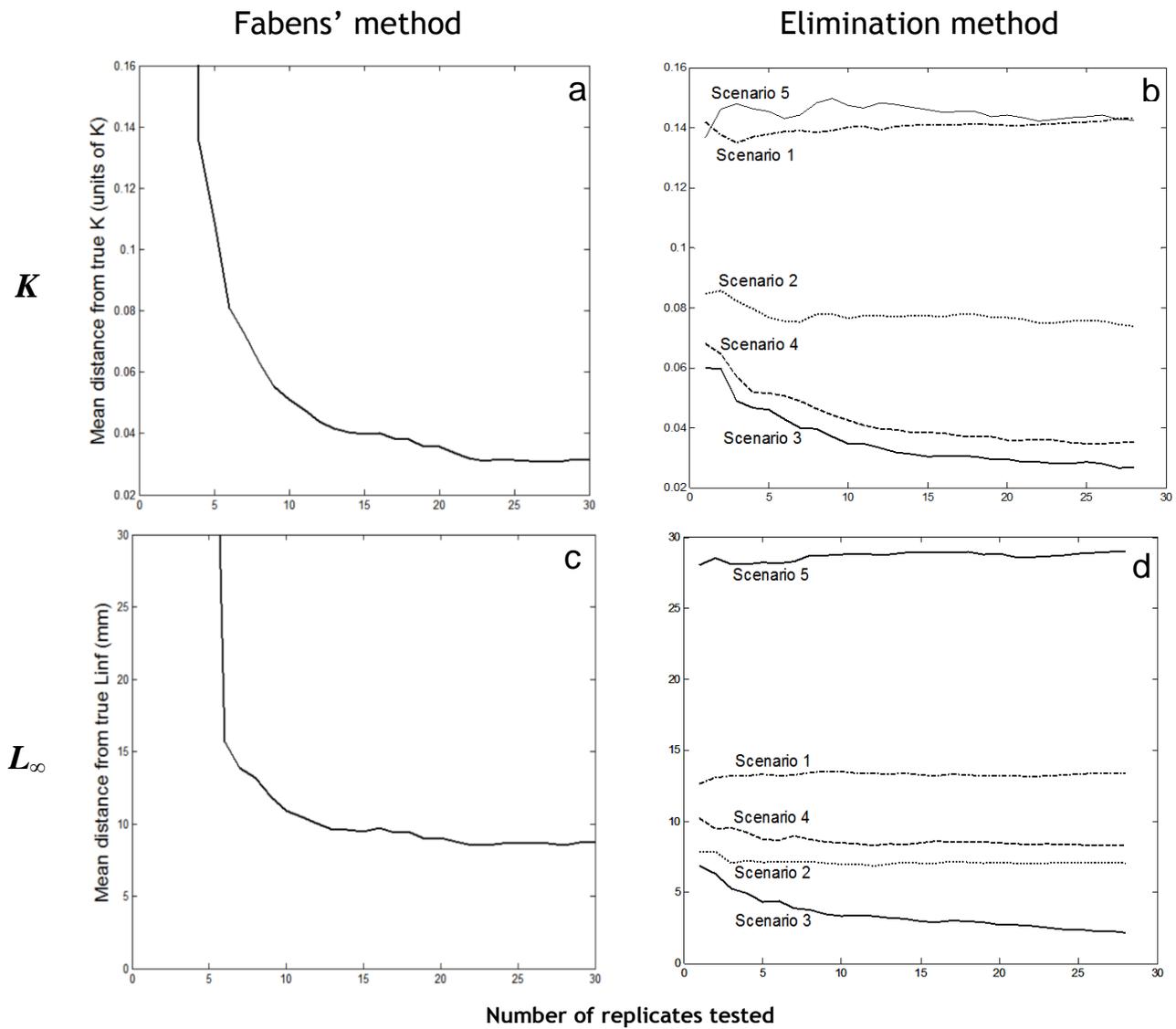


Figure 4.4 Accuracy of estimations of K (top row) and L_∞ (bottom row) produced from 100 simulations. Vertical axes show distance from ‘true’ values in units of the relevant parameter, averaged from the 100 simulations for each n replicates. Panels on the left display the results produced by Fabens’ method. Panels on the right display the results from the elimination method, curves showing the results for each of the five scenarios of varying accuracy in the ‘guesstimate’ of the plausible range. In scenario 3, the plausible range is centred correctly on true L_∞ , the ranges used in scenarios 1 and 2 are underestimates and scenarios 4 and 5 are overestimates.

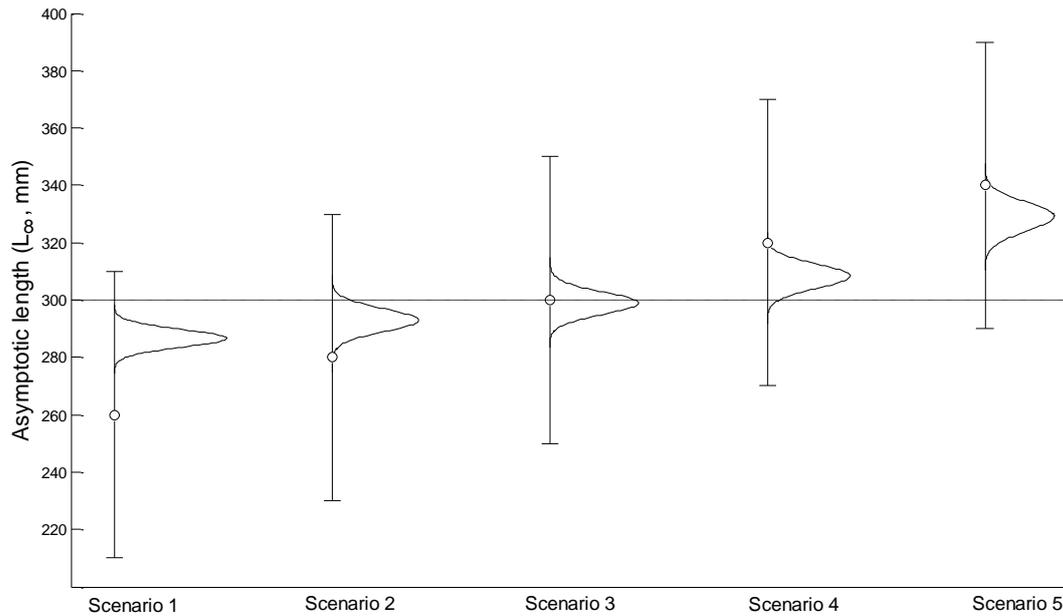


Figure 4.5 The five scenarios used to test the robustness of the fitting procedure to inaccuracy in the estimate of the plausible range for L_{∞} . The true value of L_{∞} is illustrated by the dashed line. The middle range, scenario 3, is the most accurate scenario; the two smaller and two larger ranges represent varying levels of under- and overestimation. Ranges are 100 mm wide. The distributions plotted onto each range are probability density functions of the occurrence of the fitted values of L_{∞} in each scenario, produced from 100 simulations. It can be seen that only the distribution for scenario 3 is centred within its own range and that the other distributions are shifted considerably away from the centres of their ranges (circles) towards the true value (dashed line). The level of symmetry allows the accuracy of the scenario to be assessed.

Discussion

Our simple elimination method produces relatively accurate estimates of both K and L_{∞} , assuming that the plausible range is centred on a reasonable estimate of true L_{∞} . That the veracity of this assumption may be assessed from the symmetry of the outputs considerably improves its application: when a user is unsure of the true location of L_{∞} , as they commonly would be, they would simply need to test a number of differing but overlapping plausible ranges, accepting or eliminating the candidate displacements based on these ranges, and then utilise the range whose distribution of fitted L_{∞} was located most symmetrically within its range.

Once the correct range has been determined, the estimates produced by our elimination method are as, or more, accurate than those produced by Fabens' method when 30 replicate fish were used in the analysis. However, the key advantage of the elimination method is its improved accuracy over

Fabens' method when the number of replicates is low. In our simulations, the elimination method only required ten replicates to estimate L_{∞} to 3.8 mm (accuracy of better than $\pm 1.3\%$) and K to within 0.034 (accuracy better than $\pm 7\%$). By comparison, after 10 replicates Fabens' method could only estimate L_{∞} to within 11 mm (accuracy of better than $\pm 4\%$) and K to within 0.052 (accuracy better than $\pm 11\%$). Expressed in relative terms, the elimination method demonstrated improved accuracies of 66% and 35% in the estimations of L_{∞} and K respectively. Such improved accuracy at low replication should prove helpful in the many studies in which only a small number of recaptures are obtained, as is common in tagging studies (Randall 1961). For example, Choat et al. (1996) record that only two out of 92 tagged parrotfish were recaptured during a period of field data gathering. Similarly, only one out of 48 tagged fish was recovered by Lou (1992).

Our simple statistical approach performs better than the classical and widely-applied method of Fabens and shows potential in studies where only a small number of recaptures was obtained. The method could be improved further by the incorporation of seasonality into the somatic growth rates, which often vary considerably for fishes (Pitcher and Macdonald 1973), whereby a seasonally oscillating von Bertalanffy growth curve (Pauly et al. 1992) would be used for fitting instead of the constant curve used in the present work, and this modification will form the basis of further research.

Acknowledgments

The authors would like to extend sincere thanks to Laith Yakob for advice during method development.

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5

The lionfish invasion of the Caribbean: Using isotopic inference to gain trophic perspective on competitive and predatory interactions

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Abstract

Species invasions represent one of the greatest threats to global biodiversity and ecosystem function, and yet our knowledge of the consequences for native species is alarmingly poor. The invasion of the wider Caribbean by predatory lionfish (*Pterois* spp.) is one of the most successful marine colonisations documented, but the complexity of coral reef food webs presents enormous challenges in understanding its impacts. We use stable isotope analysis (SIA) techniques to elucidate the trophic interactions between lionfish and putative competitors and prey species in the Bahamas. We first characterise the isotopic niche space of lionfish and 17 other fish species and find that our results are consistent with the known feeding ecology of the community. We go on to find that the invader is a cosmopolitan predator whose trophic position shifts among habitats, and that it ontogenetically invades the trophic space occupied by protected Nassau grouper (*Epinephelus striatus*) which may provide a barrier to invasion on patch reefs but less so on fore reefs. We also provide evidence that lionfish feed more broadly at sites where predator biomass is lower, implying that native predators may induce risk effects in lionfish populations. We conclude that SIA shows enormous potential for scrutinising invasions of highly complex trophic systems, and we discuss various interpretations of our results in the hope that our study may provide a valuable platform from which further investigations may be launched.

Keywords: species invasions, ontogenetic competition, lionfish, Nassau grouper, stable isotopes, Bayesian mixing models, non-lethal sampling

Introduction

It is widely acknowledged that invasive species represent one of the major threats to global biodiversity and ecosystem function (Fritts and Rodda 1998, Wilcove et al. 1998, Sala et al. 2000). The mechanisms through which invasive species force native species to extinction are poorly understood and yet our ability to mitigate the impacts of invasion, and to pre-empt future invasions, is contingent upon such knowledge (Gurevitch and Padilla 2004). Indeed, even the patterns of invasion remain obscure, and the full magnitude and extent of threats posed by invasive species have yet to be described, because food webs are complex and the impacts of invasive species are often difficult to disentangle from other deleterious processes (Gurevitch and Padilla 2004).

The recent colonisation of the wider Caribbean by Indo-Pacific lionfish, *Pterois* spp. (Scorpaenidae) is one of the most successful marine colonisations ever documented (Morris and Whitfield 2009). The origins of the invasion remain uncertain, but a substantial portion of the founding population may have been introduced in 1992 as a result of accidental releases of aquarium stock when Hurricane Andrew destroyed a large number of seafront properties in Florida (Courtenay 1995). The invader is now a common sight on reefs across the wider Caribbean and western Atlantic from Venezuela to Bermuda (Morris and Whitfield 2009) and the rate of spread has been particularly rapid: lionfish were first sighted in the Bahamas in 2004 but within three years they were among the most abundant fishes in the archipelago and within five years populations had reached densities eight times greater than the maxima recorded within their home range (Green and Côté 2009).

The apparent ease with which lionfish have become established across the region implies that they successfully compete for food resources with native species, and what makes the invasion of particular concern is that lionfish are extremely voracious predators. In a controlled study using experimental reef structures, Albins and Hixon (2008) found that lionfish predation reduced the abundance of juvenile fishes by 79% over a five week period. The authors also observed individual lionfish consuming up to 20 small fish in a single 30 minute period, and eating prey with body lengths two thirds of their own and the impacts on reef fish populations may prove to be catastrophic. Yet, despite the severity of the invasion, it has generated relatively few publications to date, most which have been reports of local population density or range-extensions (e.g., Meister et al. 2005, Snyder and Burgess 2007, Whitfield et al. 2007).

In an effort to elucidate trophic interactions of the invader, some workers have examined lionfish stomach contents (e.g., Morris and Akins 2009) but although such data are undoubtedly useful, they

are limited in the insights they can provide. For catholic predators such as lionfish, the data are unavoidably patchy and also tend to obscure competition for trophic energy that has occurred among the prey items themselves. For example, the stomach contents of two predators may contain differing prey species, implying that the predators do not compete. However, the prey species themselves may compete for limited resources, amounting to *de facto* competition between the predators, and such subtle interactions represent important energy pathways in complex trophic systems.

Stable isotope analysis (SIA) techniques can provide powerful tools for ecologists seeking to tease trophic relationships (Post 2002). The isotopic signatures of prey items become incorporated into the tissues of consumers (Gearing 1991), and analysis of such signatures allows robust inferences to be made about the trophic characteristics of species or assemblages. The most commonly used values in SIA studies are the ratios of heavy to light stable isotopes of nitrogen and carbon (Post 2002). The nitrogen ratio ($\delta^{15}\text{N}$) in consumer tissues changes by a predictable factor each time it moves up a trophic level, allowing the trophic position of the consumer to be elucidated from the enrichment of $\delta^{15}\text{N}$ relative to that of primary producers. Conversely, the carbon ratio ($\delta^{13}\text{C}$) in consumer tissues does not change substantially as it moves through the trophic system, creating a characteristic signal from which the photosynthetic origins of the carbon may be traced. By taking measurements of these ratios from consumers in multiple guilds, the 'isotopic niche space' of entire communities can be recreated (Newsome et al. 2007). For further information on the uses and limitations of SIA in trophodynamic studies, Post (2002) provides a valuable discussion.

Using tissue samples collected from primary food sources and fish consumers on Bahamian reefs, we analyse isotopic niche space to explore the trophic interactions within the fish assemblage in general, and of lionfish and Nassau grouper (*Epinephelus striatus*) in particular. We begin by analysing community data from patch reefs to determine how well the SIA method can detect established patterns in ecological function and habitat specialisation in feeding ecology. We then examine how trophic overlap between lionfish and Nassau grouper shifts with body size and across habitats. The Nassau grouper is a large (>100 cm) predatory fish of the family Serranidae and, classified as *Endangered* on the IUCN Red List. As one of the few known predators of lionfish in the wider Caribbean (Maljković et al. 2008) we wish to determine the extent to which it may also be a competitor of the invader, as such intraguild predation (Polis et al. 1989) may provide additional barriers to invasion success. Finally, we explore how the trophic position of lionfish changes across the boundary of an ecologically successful marine park which contains significantly elevated predator biomass (including *E. striatus*) where lionfish densities are known to be lower (Mumby et

al. 2011). With the exception of the invader, all fish tissue was sampled using non-lethal methods, allowing us to study protected Nassau grouper as well as ecologically important grazing species without exacerbating the ecological degradation which burdens modern Caribbean reefs.

Methods

Fieldwork was conducted at nine fore reefs sites inside and outside the Exuma Cays Land and Sea Park (ECLSP), and at two patch reef sites outside the park (Figure 5.1). The Exuma Cays Land and Sea Park is a large (442 km²) and ecologically successful marine reserve (Mumby et al. 2007). At the time of data collection, lionfish were not a fisheries target in the Bahamas and we would not expect to see a direct effect of fishing on unprotected populations. However, the park contains a substantially greater biomass of large predators than surrounding areas that are not under protection (Mumby et al. 2011) and we examine lionfish isotope data from similar fore reef habitats inside and outside the park. Patch reefs were adjacent to seagrass beds comprised of *Thalassia testudinum* and *Syringodium filiforme*. Some of the study species, such as Nassau grouper and parrotfishes, are of high conservation value and so all species but lionfish were sampled non-lethally. Fin clippings were taken from all fish, the isotopic signatures of which compare very well with lethally-sampled muscle tissue (Kelly et al. 2006). Clippings were taken from the posterior part of the dorsal fin rather than the tail fin, as terminal phase males often display elaborately adorned tail fins, which may be assumed to have meaning in courtship. In exploratory samplings, fish did not appear to suffer discomfort from the removal of clippings, and a number of sampled fish were subsequently re-sighted during the course of the study and did not appear to be impaired relative to unsampled conspecifics.

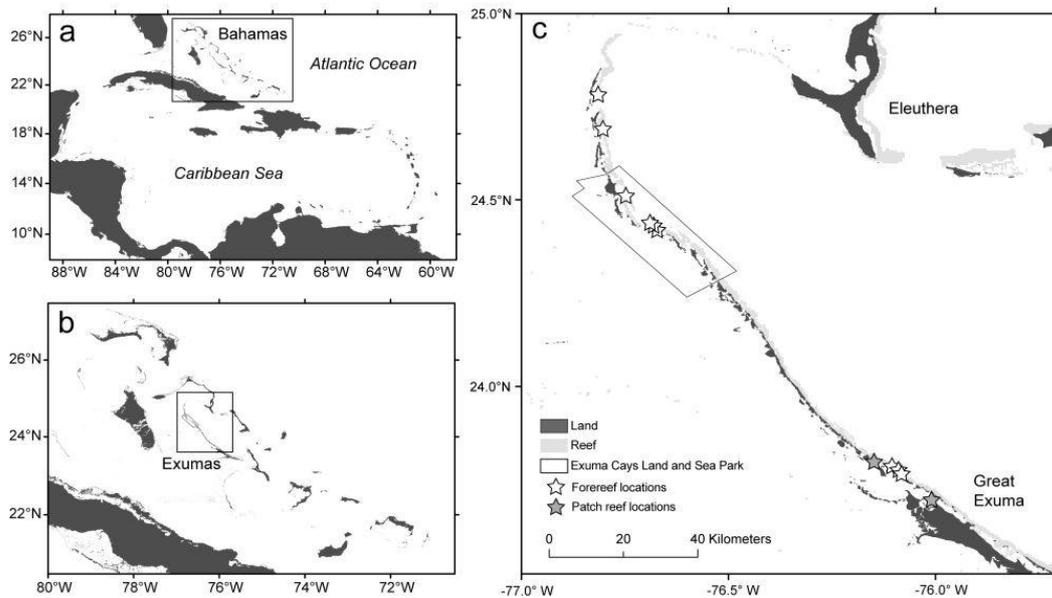


Figure 5.1 Locations of field sampling sites in Exuma Cays, Bahamas. The dataset contains nine fore reef sampling locations (panel c, white stars) from inside and outside the Exuma Cays Land and Sea Park (panel c, polygon), and two patch reef locations (panel c, grey stars).

Sampling of fish tissue

Lionfish were caught using pole spears but other fish were caught with traps, seine nets, hand nets, and/or quinaldine (2-methylquinoline) anaesthetic mixed with equal parts ethanol (95%) and delivered using 60 ml syringes fitted with 10cm lengths of silicone tubing. Tubing could be inserted into small gaps in the substrate, and also could be loosely knotted to restrict leakage. Syringes were loaded on the boat before dives, but could also be refilled underwater from a Ziploc bag filled with quinaldine. After capture, fish were retained in mesh holding bags. Processing was generally undertaken *in situ* on sandy benthos, although when dive time was limited the fish were slowly raised to the surface then brought onto the boat and held in a large (< 100 L) cooler bin filled with seawater that was regularly replenished to ensure water remained oxygenated.

Around 1.5 mg dry weight (approximately 50 mg wet weight) of fin tissue was required to provide the two aliquots of tissue per fish that were necessary for SIA, and the approximate dimensions of such a clipping had been estimated previously using fin tissue from a rainbow trout (*Oncorhynchus mykiss*) in the University of Exeter wet lab. To ensure that a large enough clipping would be taken from fish of varying body sizes throughout of the duration of the fieldwork and to mitigate the magnifying effect of water, a visual size reference was carried.

Fin clippings were stored temporarily in snap-shut 1.5 ml micro-centrifuge tubes (hereafter referred to as 'vials') that were glued into plastic vial trays to make underwater sampling racks. A sampling station was made by attaching the rack, scissors, measure, slate and small mesh bag to a 1 kg dive weight. The station was placed near the sampling nets, but out of the line of sight of fish being corralled towards the nets so that one diver could sample fin clippings whilst the others continued to catch fish. Once each sample was safely stored, the fork length of the individual was recorded and the fish was released. By the end of the fieldwork period, processing time for a diver working unassisted was approximately one minute per fish.

Sampling of primary producers

Six to eight algae samples were collected at each site of *Dictyota* spp., *Lobophora* spp., *Cladophora* spp and algal turfs (various taxa). The seagrasses *Syringodium filiforme* and *Thalassia testudinum* were also sampled adjacent to patch reefs. All plant samples were thoroughly cleaned of epiphytes. Phytoplankton were sampled using a plankton net towed behind the dive boat. The net had an aperture diameter of 50 cm, was 4 m long, and had a mesh size of 100 μm . Attached to the 'cod end' of the net was a cylinder containing small (~50 cm length, 100 μm mesh size) sampling nets which were changed after each tow. Tows lasted for ~12 minutes after which the sampling net was removed and sealed in a clean plastic container. At the end of each day, plankton nets were washed out using fresh water as salt water may have contaminated the samples with additional microalgae. Samples were fractionated through sieves of 200 μm and 105 μm , the larger fraction being discarded and smaller fraction being drained and scooped onto squares of aluminium foil. Filter paper could not be used as it contains carbon and may have contaminated the isotopic signal and so samples were arranged on clean plastic trays, which were covered to prevent contamination by insects etc. After drying for approximately 48 hours, samples were individually placed into clean, numbered vials and silica gel beads were added to each before being sealed.

Sample processing

Fin clippings are composed of a mixture of skin and ray tissue, which likely vary in the rate of isotopic fractionation that takes place. In larger fish it would be possible to sample skin tissue alone by snipping from the fin margin edge of the clippings where the ratio of skin to ray is very high, but this would not be possible with small fish such as bluehead (*Thalassoma bifasciatum*) whose entire sample was required to achieve the necessary mass for spectrometry. For this reason, samples were

taken from the edge farthest from the margin so that all samples were a homogenized mixture of skin and ray tissue. The desiccated clippings were snipped to fine particles which were then scooped into tin capsules (5 x 3.5 mm) and weighed to 0.7 mg ($\pm 10\%$) on a microbalance. Algae and seagrasses were pulverised and weighed to 3 mg ($\pm 10\%$). Isotope signatures of samples were determined at the Natural Environment Research Council (NERC) Life Sciences Mass Spectrometry Facility, East Kilbride, Scotland.

Data analysis

The ratios of heavy to light isotope of each element in the consumer tissues were expressed relative to a standard in δ notation such that:

$$\delta^h E = \left[\left(\frac{{}^h E / {}^1 E_{\text{sample}}}{{}^h E / {}^1 E_{\text{standard}}} - 1 \right) \times 1000 \right]$$

where ${}^h E$ and ${}^1 E$ are respectively the heavy and light stable isotopes of element E . The isotopic signal in consumer tissues is commonly the aggregate of a mixture of food sources (Inger and Bearhop 2008), so to estimate the contribution of various sources to the signal the data were analysed using a Bayesian mixing model, SIAR (Parnell et al. 2008). Such Bayesian approaches to solving signal mixing problems are currently revolutionising the use of stable isotopes in dietary studies, in much the same way as they have done for molecular ecology (Moore and Semmens 2008, Jackson et al. 2009).

Mixing models allow for the estimation of the most likely proportional contributions of isotopic sources to consumer tissue signal, from which dietary composition may be inferred. Bayesian mixing models have the advantage of allowing informative priors to guide model estimates, explicitly accommodating many of the uncertainties that have been a problem for some applications of SIA in the past (Rutz et al. 2010, Jackson et al. 2011). For example, when the number of dietary sources exceeds the number of isotopes plus one, there is no exact solution to a mixing problem. In ecological studies, this is frequently the case. Although some existing mixing models can incorporate multiple dietary sources, they cannot accommodate uncertainty; other models have the opposite constraint. SIAR can handle both uncertainty and multiple sources, providing a robust estimate of the most likely solution rather than simply producing a range of feasible solutions, as many other models do. A further advantage of SIAR is that it includes an overall residual error term into which unexplained variance may be apportioned, as found in even the most basic linear

models but absent from other Bayesian mixing models. For a useful discussion of mixing models in general and SIAR in particular, please see Parnell et al. 2010.

Monte Carlo simulations were used to test for differences in the ranges of isotope values between habitats. First, the difference between isotope standard deviations between the two habitats was calculated, which was used as the test statistic. Data were then pooled and randomly split into two groups, and the difference between the two resulting standard deviations was calculated. The process was repeated 10^4 times, and a distribution was built from the results. The test statistic was then compared against the distribution to determine how frequently a value of the observed magnitude would occur by chance alone.

Results

1. *Patch reef community isotopic niche space*

Only one or two individuals could be sampled from a number of taxa, including coney (*Cephalopholis fulva*), longspine squirrelfish (*Holocentrus rufus*), red hind (*Epinephelus guttatus*), white grunt (*Haemulon plumieri*) and princess parrotfish (*Scarus taeniopterus*). Although robust conclusions cannot be drawn from such data, they are included here as they occupy isotopic positions that compare favourably with those of taxonomically or functionally similar species in the dataset, and the paucity of stable isotope work on coral reef fishes may make them of some interest. To improve the accuracy of the mixing model outputs, we reduce the taxonomic resolution of the data by classifying species into larger groups based on known trophic function (Table 5.1).

Table 5.1 Taxa and number of samples of tissue items contained in the stable isotope dataset. Because there were very few samples for some fish species, these data were aggregated into classes for mixing model analysis, based on taxonomic and/or functional similarities.

Item	Number of samples	Fish class for mixing model analysis	Number of samples in fish class
Phytoplankton	13	-	-
<i>Thalassia testudinum</i>	12	-	-
<i>Syringodium filiforme</i>	11	-	-
<i>Cladophora</i> spp.	12	-	-
<i>Dictyota</i> spp.	10	-	-
<i>Lobophora</i> spp.	6	-	-
Algal turfs	8	-	-
Lionfish (<i>Pterois</i> spp.)	17 (patch reefs) 37 (fore reefs)	Lionfish	17
Nassau grouper (<i>Epinephelus striatus</i>)	14	Not used in mixing model	-
Coney (<i>Cephalopholis fulva</i>)	1	Small groupers	3
Red hind (<i>Epinephelus guttatus</i>)	2		
French grunt (<i>Haemulon flavolineatum</i>)	16	Benthic invertivores (habituate reefs, but forage for invertebrates in seagrass benthos)	20
White grunt (<i>Haemulon plumieri</i>)	1		
Spotted goatfish (<i>Pseudupeneus maculatus</i>)	2		
Longspine squirrelfish (<i>Holocentrus rufus</i>)	1		
Beaugregory (<i>Stegastes leucostictus</i>)	11	Small generalists (aggregate above and around coral heads, and feed on zooplankton and/or algal turfs)	23
Bluehead wrasse (<i>Thalassoma bifasciatum</i>)	7		
Sergeant major (<i>Abudefduf saxatilis</i>)	5		
Blue tang (<i>Acanthurus coeruleus</i>)	10	Surgeonfishes	18
Ocean surgeon (<i>Acanthurus bahianus</i>)	8		
Striped parrotfish (<i>Scarus iserti</i>)	19	Scraping parrotfishes	22
Queen parrotfish (<i>Scarus vetula</i>)	2		
Princess parrotfish (<i>Scarus taeniopterus</i>)	1		
Redband parrotfish (<i>Sparisoma aurofrenatum</i>)	10	Excavating parrotfishes	13
Stoplight parrotfish (<i>Sparisoma viride</i>)	3		

When the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data are plotted, the study taxa fall into coherent ecological clusters (Figure 5.3). The piscivore guild (lionfish, Nassau grouper, coney and red hind) occupies the highest (most $\delta^{15}\text{N}$ enriched) position, followed by the invertivore guild, which overlaps with the upper range of the herbivore guild. In reality, many reef fishes do not fit neatly into a single guild and some of our

‘invertivore’ species supplement their diet with algae (Cervigón et al. 1993). With this in mind, the ‘invertivore’ guild noticeably splits along the $\delta^{13}\text{C}$ axis into those that live around coral heads and feed on reef zooplankton and turf algae, and those that forage in or near the sandy benthos of seagrass beds. For convenience, we name the former group ‘the small generalists’ and the latter group ‘the seagrass invertivores’. The small generalist group consists of a wrasse (bluehead, *Thalassoma bifasciatum*) and two damselfishes (sergeant major, *Abudefduf saxatilis*; beaugregory, *Stegastes leucostictus*), and is offset towards the relatively low $\delta^{13}\text{C}$ isotopic space of phytoplankton and benthic algae. The seagrass invertivores consists of two grunts (French grunt, *Haemulon flavolineatum*; white grunt, *H. plumieri*), a goatfish (spotted goatfish, *Pseudupeneus maculatus*) and a squirrelfish (longspine squirrelfish, *Holocentrus rufus*), and is offset towards the higher $\delta^{13}\text{C}$ space of seagrasses.

The surgeonfishes (blue tang, *Acanthurus coeruleus*, and ocean surgeon, *Acanthurus bahianus*) cluster tightly and represent the lowest $\delta^{13}\text{C}$ of any of our fish species. Although they occupy space above reef algae, they are enriched in $\delta^{15}\text{N}$ compared to the other herbivores, the parrotfishes, which occupy the five lowest positions in $\delta^{15}\text{N}$ space. The parrotfishes also break into two functional groups by feeding mode along the $\delta^{13}\text{C}$ axis, although less clearly so than the invertivores. The two excavating species, stoplight (*Sparisoma viride*) and redband (*Sp. aurofrenatum*) parrotfish, graze predominantly on macroalgae (Randall 1967) and are in $\delta^{13}\text{C}$ terms more similar to those macroalgae than are the three scraping species, queen (*Scarus vetula*), princess (*Sc. taeniopterus*) and striped (*Sc. iserti*) parrotfish, which concentrate on algal turfs with which their $\delta^{13}\text{C}$ signals are more similar. Corallimorph tissue could not be separated in the field into its constituent animal (polyp) and plant (symbiotic dinoflagellates) components, and the data therefore represent the entire holobiont.

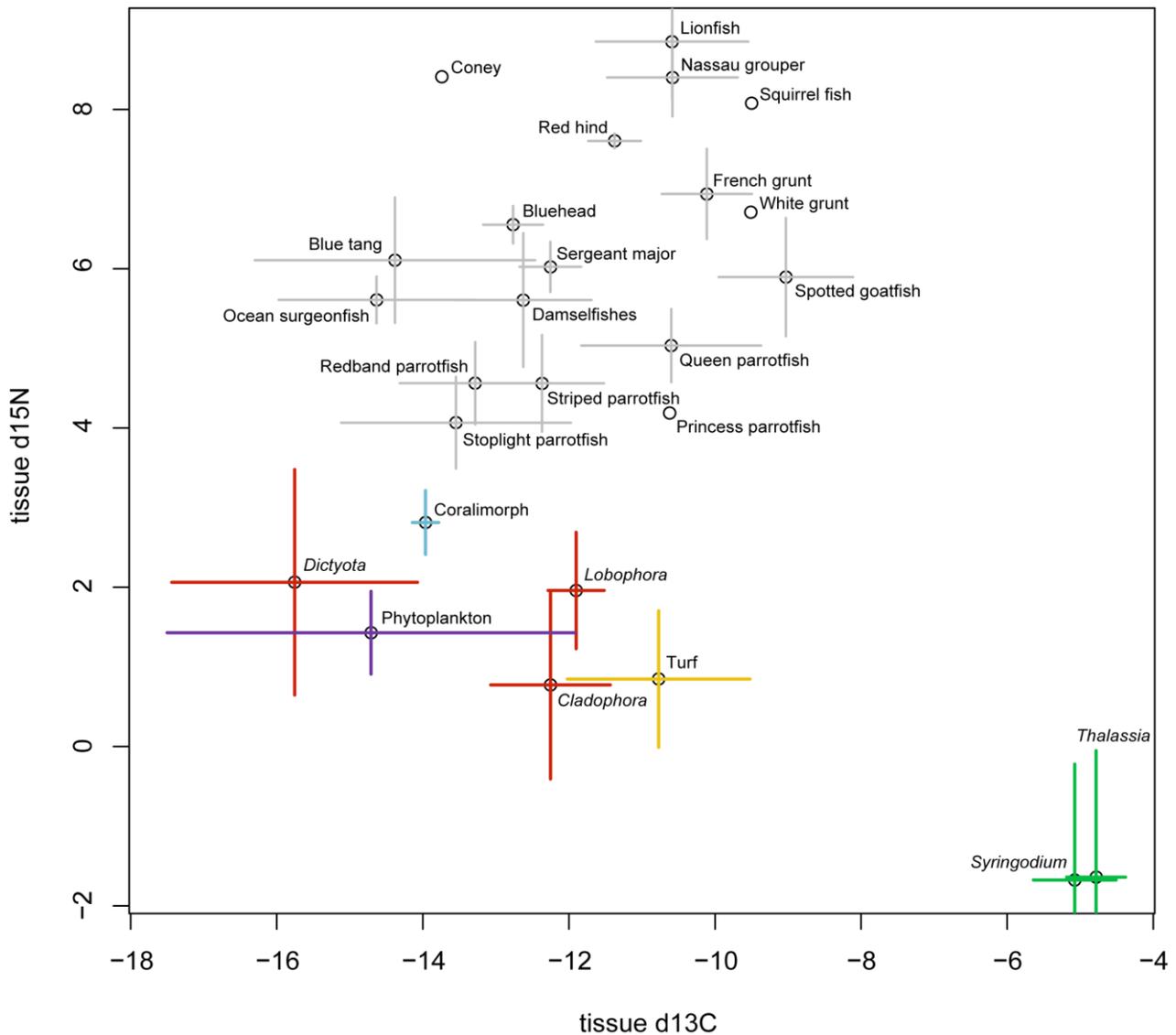


Figure 5.3 Tissue isotope signatures from members of two coral patch reef communities in the Bahamas. $\delta^{15}\text{N}$ axis shows enrichment in consumer tissues of the heavier nitrogen isotope as trophic energy moves upwards. $\delta^{13}\text{C}$ axis indicates variation of source carbon in primary producer tissues: green, seagrasses; red, macroalgae; yellow, algal turfs; blue, phytoplankton; cyan, corallimorphs. Error bars are standard deviations of field data.

Running the SIAR mixing model on the data allows us to partition out the likely proportional contributions of food sources to various consumers. By classifying the fish species into groups based on taxonomic and/or functional similarity (Table 5.1 and Figure 5.4a) we use the mixing model to estimate the proportion that each group contributes to the diet of the invasive lionfish (Figure 5.4b and 5.4c).

Proportion of fish sources in lionfish diet

The seagrass invertivores (grunts, goatfish and squirrelfish) constitute the largest carbon contribution to the lionfish diet of any group, followed by the small groupers (Figure 5.4b).

Because lionfish are such cosmopolitan omnivores (Morris and Akins 2009) they may exhibit intra-guild predation with other predatory fishes, whereby they are simultaneously predators and competitors (Polis et al. 1989). Although it may be possible to separate lionfish predation from competition for the invertivores, it is not possible to do so for the small groupers. Because the small groupers and the seagrass invertivores dominate the mixing model results, for exploratory purposes we drop them out of the dataset and run the mixing model only on the species with which the lionfish do not compete and thus can only be predators (Figure 5.4c). The outputs show the strongest signal is produced from the small generalists (damselfishes and wrasse), followed by the scraping parrotfishes (queen, princess and striped). The excavating parrotfishes (stoplight and redband) and the surgeonfishes (blue tang and ocean surgeon) contribute little to the lionfish signal.

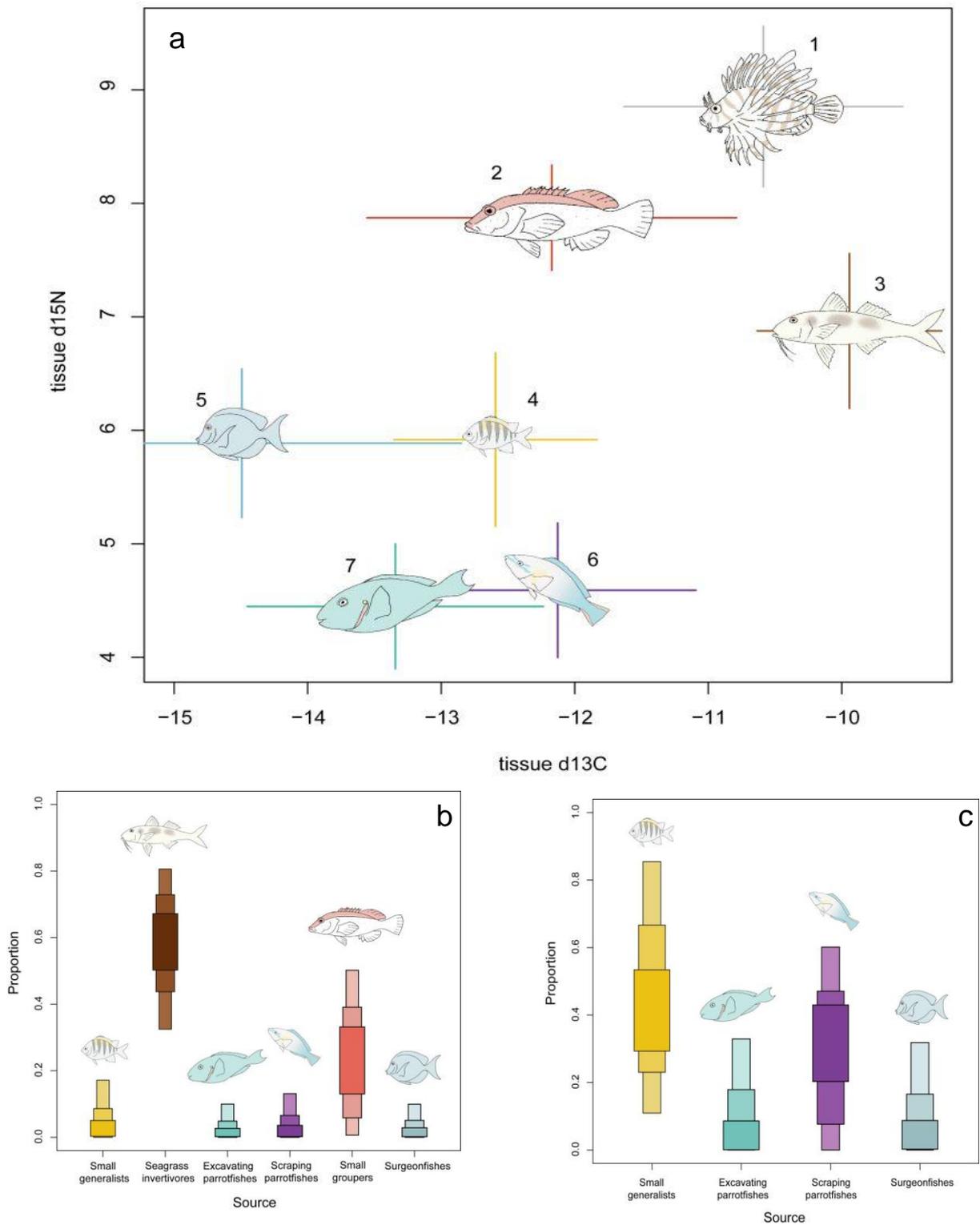


Figure 5.4 Isotopic niche space of lionfish and putative prey groups, classified by taxonomic and/or functional similarity (panel a and Table 5.1) and proportional contributions of fish groups to lionfish diet (panels b and c). Icons show representative species from each group. 1, *Lionfish*; 2, *Small groupers*; 3, *Seagrass invertivores*; 4, *Small generalists*; 5, *Surgeonfishes*; 6, *Scraping parrotfishes*; 7, *Excavating parrotfishes*. Panel b shows the results of the SIAR mixing model run for the fish groups, with bars representing the Bayesian credible ranges of the contribution of groups to lionfish diet. Panel c shows the SIAR output run only using the groups that are known not to be lionfish competitors, namely the small generalists and the three herbivore groups.

2. *Lionfish and grouper isotopic niche space within and across habitat types*

Lionfish and Nassau grouper overlap almost completely in δ -space on patch reefs (Figure 5.3) and it is likely that they compete for food resources. We first examine habitat-specific shifts in δ -space overlap with Nassau grouper to see if competition may pose a greater barrier to invasion in one habitat than another. To minimise confounding effects caused by differential fishing, all of the data used in this section were from sites outside the ECLSP boundary, and there is no significant difference in body size between patch and fore reefs in our data for either lionfish ($t_{[19]} = 1.842$, $P = 0.089$) or Nassau grouper ($t_{[12]} = 1.546$, $P = 0.147$).

Within each habitat, we divide the lionfish data into two groups by body size, ‘small’ and ‘large’, around the median length, 26.5 cm. Plotting the δ -space of the lionfish size classes in each habitat against the δ -space of Nassau grouper implies a substantial shift in trophic overlap across habitats (Figure 5.5). On patch reefs, small and large lionfish share almost identical δ -space (Figure 5.5a) and both overlap with Nassau grouper. On deeper fore reefs, however, large lionfish continue to overlap with Nassau grouper but small lionfish much less so (Figure 5.5b).

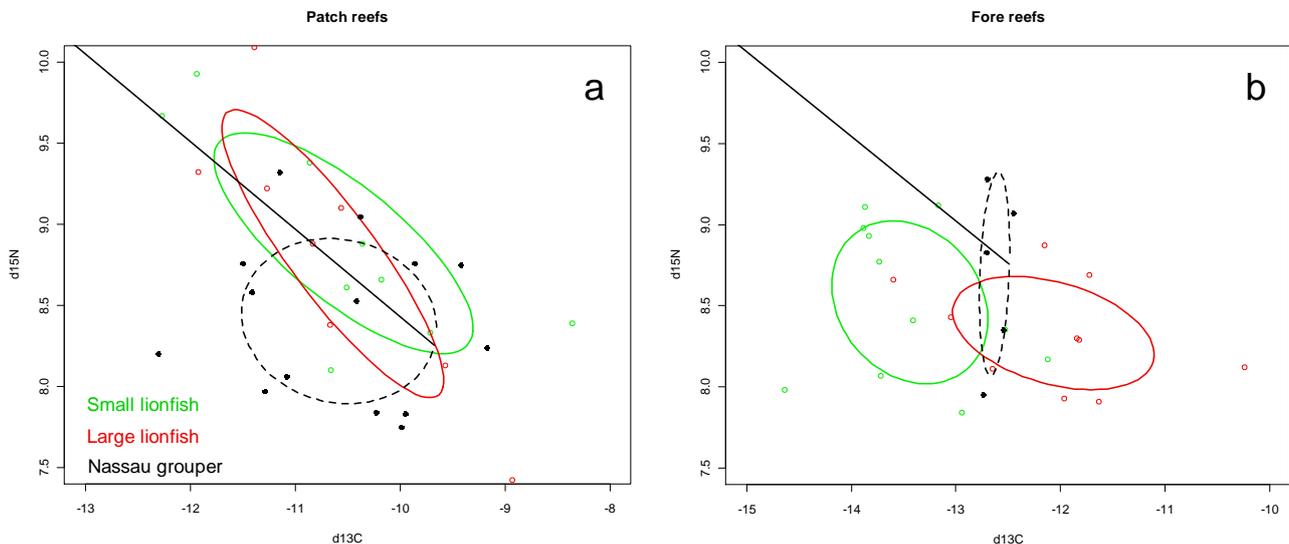


Figure 5.5 Changes in the overlap in isotopic niche space of lionfish and Nassau grouper across two habitat types, shallow, low-productivity patch reefs (panel a) and deeper, high-productivity fore reefs (panel b). Points represent tissue isotope data from individual fish, overlaid with standard ellipses which may be considered bivariate analogies to standard deviations in univariate data. Note that the horizontal scale varies.

To examine patterns of the lionfish isotopic signal in more detail, we examine changes in lionfish isotopic signal as a continuous function of body size. Lionfish do not show a consistent enrichment in $\delta^{15}\text{N}$ with body size either on patch reefs ($F_{[1,15]} = 1.807$; $P = 0.198$) or on fore reefs ($F_{[1,19]} =$

0.01; $P = 0.946$). However, lionfish do exhibit a strong shift in the carbon isotope ($\delta^{13}\text{C}$) with body size on fore reefs ($F_{[1,19]} = 17.45$; $P < 0.001$; $r^2 = 0.45$), though not on patch reefs (Figure 5.6).

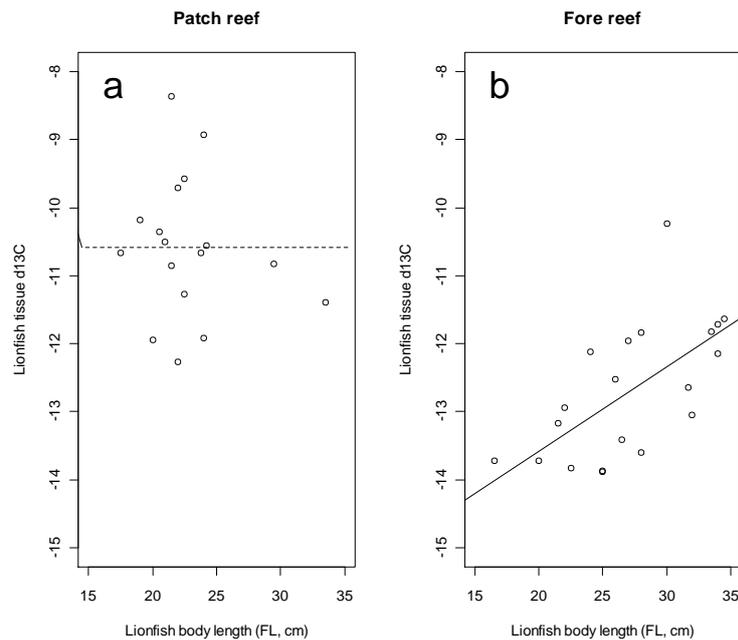


Figure 5.6 Tissue $\delta^{13}\text{C}$ as a function of lionfish body size across two habitats, shallow patch reef (panel a) and deeper fore reef (panel b). Lines show linear model fits to each subset of data, showing a significant $\delta^{13}\text{C}$ increase with size in fore reef habitats but not in patch reefs. No significant trend was observed in $\delta^{15}\text{N}$ with body size in either habitat.

3. *Lionfish isotopic niche space across a predation gradient*

Lionfish body length does not differ significantly across the boundary of the Exuma Cay Land and Sea Park (Wilcoxon $W = 67.5$; $n = 10$ and 11 ; $P = 0.397$). However, the trophic niche space of lionfish differs significantly between populations inside the park and those outside (Figure 5.7a). The mean value of $\delta^{15}\text{N}$ is significantly higher for lionfish outside the Park ($t_{[17]} = -3.003$; $P = 0.008$), but the difference in the mean value of $\delta^{13}\text{C}$ is marginal ($t_{[17]} = -1.907$; $P = 0.077$). The plot also suggests there may be a difference in the breadth of the range of values recorded for each isotope ratio across the boundary. Conducting Monte Carlo simulations to determine how often the observed difference (Δ) in standard deviations was likely to have occurred by chance alone at the 95% confidence level, we find that for $\delta^{15}\text{N}$, $\Delta = -0.178$ which occurs less frequently than the 0.025 quantile value of -0.173 (Figure 5.7b), meaning it is unlikely to have occurred by chance. For $\delta^{13}\text{C}$, however, $\Delta = 0.509$ which occurs more frequently than the 0.975 quantile value of 0.584 (Figure 5.7c), and a difference of such magnitude is thereby attributable to chance.

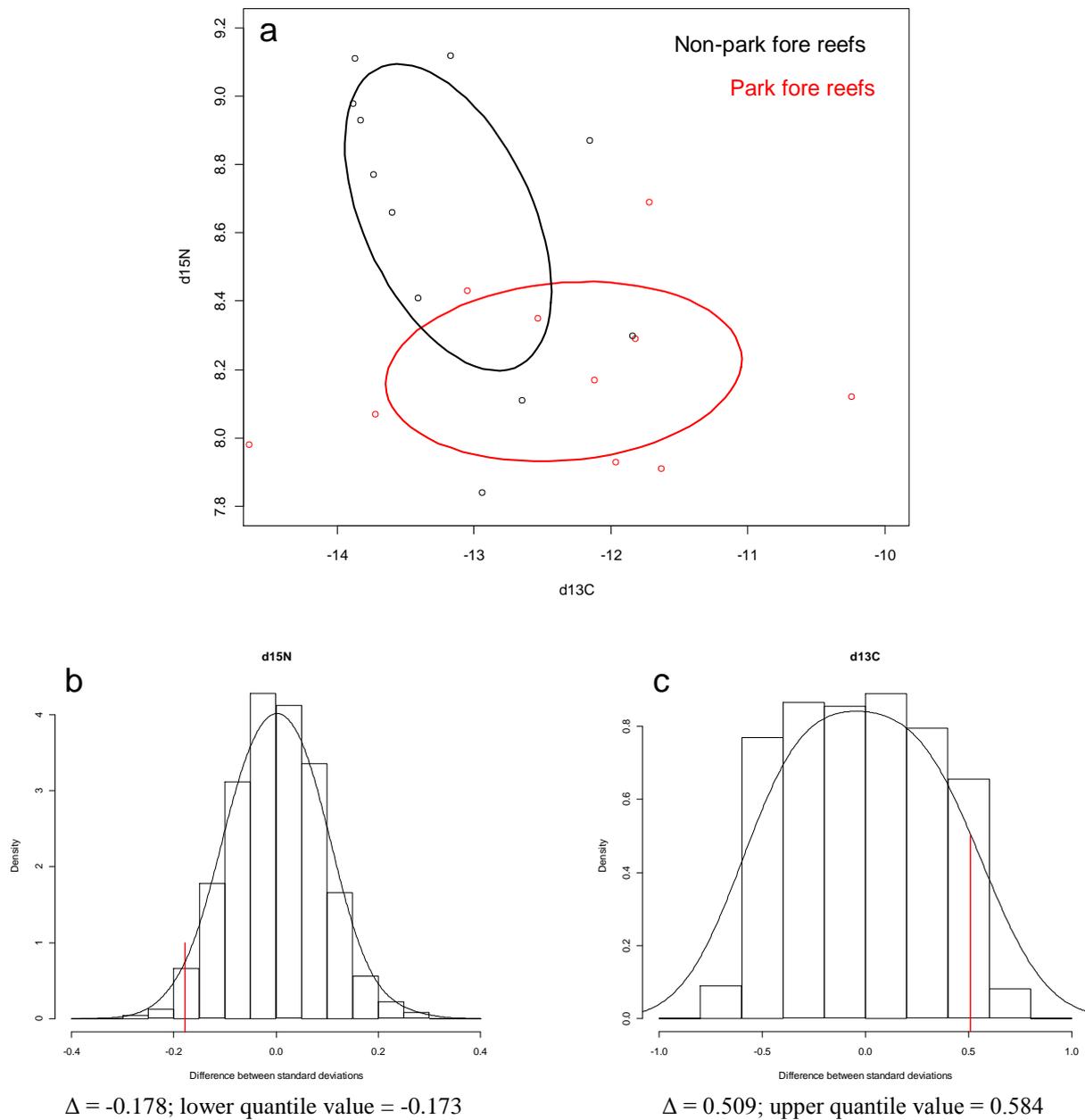


Figure 5.7 Changes in the isotopic δ -space of invasive lionfish on fore reefs across the boundary of the Exuma Cays Land and Sea Park, which contains a substantially greater biomass of large predators than surrounding non-park areas. There was no significant difference in lionfish body size between treatments. Panel a shows isotopic niche space, with plotted features as in Figure 5.5. $\delta^{15}\text{N}$ appears to cover a wider range of values outside the Park but conversely $\delta^{13}\text{C}$ appears broader inside. Panels b ($\delta^{15}\text{N}$) and c ($\delta^{13}\text{C}$) show the results of Monte Carlo simulations to determine the likelihood of achieving the difference in standard deviations by chance alone. Red lines show the location of the test statistic, Δ , which is the magnitude of the observed difference in standard deviations across the Park boundary.

Discussion

Our isotope data cluster into ecologically meaningful groups that are consistent with the known feeding ecology of many of the study species, lending confidence in the utility of stable isotope methods for the study of coral reef trophodynamics in particular, and complex ecosystems in general. The results also support the use of non-lethal fin clippings in the study of fishes, demonstrating that such tissues can provide insights to feeding ecology that may not be apparent through traditional approaches. Caribbean surgeonfishes (Acanthuridae), for example, are generally considered to eat turf and filamentous algae (Randall 1967, Böhlke and Chaplin 1993) plus sediment and detritus (Robertson 1991). It is therefore surprising that surgeonfishes should occupy a considerably higher $\delta^{15}\text{N}$ trophic position than herbivorous parrotfish. It is unlikely that the signal is driven by detritus alone, as parrotfish must also ingest large quantities of detritus whilst grazing on algae, yet the surgeonfish tissue is so enriched in $\delta^{15}\text{N}$ that they share a trophic level with the zooplanktivores.

Elevated $\delta^{15}\text{N}$ in grazing fish tissues has previously been demonstrated by Mill et al. (2007), who found that three herbivores from Oman exhibited higher $\delta^{15}\text{N}$ levels than would have been expected, and the authors found no evidence of animal matter in gut contents. They conclude that the herbivores do not supplement their diet with animal protein, pointing out that herbivorous fishes consume around 20% of their body weight in food per day compared with only 3-4% for piscivorous fishes (Horn 1989), so herbivores may compensate for food resources that are low in nitrogen by elevated consumption. Although this finding could explain why surgeonfish may be enriched in $\delta^{15}\text{N}$, it does not satisfactorily explain why the surgeonfish values in our data are so much higher than the parrotfish values, which should be similarly enriched.

A possible explanation for the observed enrichment is offered by the fact that surgeonfishes spend a considerable amount of their time foraging on sandy substrate, where they have been presumed to feed on detritus (Robertson 1991). In addition to detritus, reef sediment contains high densities of zooplankters that seek refuge in the benthos during daylight, emerging at night to feed in the water column (Jacoby and Greenwood 1988). The same is true of gnathiid isopods, which are important parasites for many coral reef fishes, emerging to feed before returning to their benthic refuge (Grutter et al. 2000). If surgeonfish ingest and assimilate such invertebrates, their $\delta^{15}\text{N}$ signal may be more similar to other invertivores such as bluehead wrasses than to parrotfishes, as is the case in our dataset. Indeed, despite the fact that isopod parasites are subordinate to fishes in terms of biological complexity, their tissue isotope signal may be higher because consumers are enriched in

$\delta^{15}\text{N}$ relative to their food source, in this case, host fishes. It is known that juvenile blue tang (*Acanthurus coeruleus*) perform a cleaning function by eating parasites from green turtles (Sazima et al. 2004) and adults may retain the capacity to digest such food sources, even though they may no longer act as cleaners. Surgeonfishes may therefore occupy their unexpectedly high trophic position by consuming $\delta^{15}\text{N}$ enriched isopods in the benthos, and may even play a hitherto unknown role in controlling populations of reef fish parasites.

One of the greatest challenges in teasing apart the trophic impacts of the lionfish invasion using any methodology lies in the fact that the species is a generalist predator, and feeds on a wide range of invertebrate and vertebrate taxa (Morris and Akins 2009). Indeed, the great breadth of its diet may be a key factor in explaining the success of lionfish in invading Atlantic ecosystems. The fluctuating resource availability theory (Davis 2003) contends that exotics can become established in a new community when resource fluxes create ephemeral opportunities for entry. In this situation, a successful invader needs neither to outcompete nor to be niche differentiated from natives, but simply to be in the right place at the right time to exploit fluctuating resources. The arrival of settling fish to coral reefs is highly variable in space and time (Sale 1977). When supply is low there will be increased competition per unit of resource, acting as a barrier to invasion, but a surplus would act to reduce competition, and an introduced species may gain a foothold and become established.

Although the SIAR mixing model results imply that lionfish gain much of their carbon from the pathway of invertivores such as grunts, we cannot tell with certainty that lionfish actually consume grunts, as lionfish also directly consume invertebrates, and it is hard to say from the data if the invader is a predator of invertivores, or a competitor, or both. However, by incorporating additional knowledge of the various species, we may gain additional insight. Given the specialised anatomical adaptations required for their ambush mode of predation (Morris and Akins 2009) it is unlikely that lionfish dig in the sandy benthos for invertebrates, as do members of the invertivore group, and the predator would not gain seagrass carbon by consuming sandy benthos invertebrates. Instead, lionfish probably prey on reef invertebrates in the same manner as they prey on reef fish, where the predator corrals and traps prey against the complex substrate (Morris and Akins 2009). Since reef invertebrates will reflect the low $\delta^{13}\text{C}$ signal of the reef macroalgae, the relatively high $\delta^{13}\text{C}$ signal of the lionfish does indeed imply that they assimilate seagrass carbon, which must be through consumption of seagrass-foraging invertivores, and thus they are more likely to be predators of these fishes than competitors.

Lionfish do not show a consistent enrichment in $\delta^{15}\text{N}$ with body size in either habitat, which refutes the intuitive hypothesis that they may feed ‘further up’ the trophic system as they grow larger. However, the strong shift in tissue $\delta^{13}\text{C}$ with body size in fore-reef-dwelling lionfishes is particularly interesting, especially as the shift does not occur on patch reefs. There are three important differences in our fish groups between these habitats which are consistent with an ontogenetic shift in lionfish diet based on prey availability. Firstly, we would expect a greater availability of plankton-eating small generalists on high-productivity fore reefs than on low-productivity patch reefs. Secondly, our results show that the small generalists have lower $\delta^{13}\text{C}$ signals than the seagrass invertivores. Thirdly, the small generalists are considerably smaller bodied than the seagrass invertivores (mean fork lengths are 10.94 cm and 16.48 cm respectively; $t_{[35]} = -6.08$; $P < 0.001$). A parsimonious explanation for the habitat-specific ontogenetic shift in lionfish $\delta^{13}\text{C}$ is that juvenile lionfish on fore reefs prey on the abundant small generalists, switching diet to larger invertivores as they grow. Such a shift would not be reflected in the lionfish $\delta^{15}\text{N}$ signal, as our results show that both the small generalists and seagrass invertivores groups feed at the same trophic level. Lionfish would not undergo this ontogenetic shift on patch reefs where small generalists are relatively uncommon, and instead they may concentrate their foraging on juvenile fishes which are plentiful in adjacent seagrass beds. This hypothesis relies on the assumption that the phytoplankton and seagrass $\delta^{13}\text{C}$ signals do not change substantially between habitats. Although there were, predictably, no seagrasses on our fore reef sites and thus we cannot compare seagrass signals, the median $\delta^{13}\text{C}$ signals for phytoplankton are not significantly different between the habitats (Wilcoxon $W = 274$; $n = 22$ and 24 ; $P = 0.812$).

Further support for the hypothesis that lionfish prey more heavily on small generalists on fore reefs than do Nassau grouper is provided by inter-specific differences in foraging methods. Nassau grouper tend to stay close to the benthos and forage within the dark crevices positioned low on coral heads. Although lionfish are also found within low crevices, they are commonly seen perching in or near crevices positioned high on coral heads which is the preferred habitat of the small generalist damselfishes and wrasses. Nassau grouper are less likely to encounter, and by extension, to consume small generalists on fore reefs, providing less of a barrier to invasion success than on patch reefs where small lionfish may have to compete with them for limited food resources.

There are significant differences in the $\delta^{15}\text{N}$ signals across the boundary of the Exuma Cays Land and Sea Park, although the same was not true of $\delta^{13}\text{C}$. Non-park lionfish are relatively enriched in $\delta^{15}\text{N}$, implying that they feed at a higher average trophic level than park lionfish. The results also show that lionfish outside the ECLSP feed over a wider range of $\delta^{15}\text{N}$ values. Although there is a

difference in the abundance of prey fish species across the boundary (Harborne et al. 2008), there are more species inside the park, and so the bias strengthens rather than confounds the result. Our findings are consistent with a scenario where large predators constrain lionfish feeding, whether through direct competition for resources and/or through ‘risk effects’ (Heithaus et al. 2008) that reduce lionfish foraging efficiency when they cannot feed as freely in the presence of higher predator densities. Although we did not collect behavioural data, the authors observed that lionfish within the Park were distinctly more skittish than those outside which could almost be touched without provoking a reaction (Mumby et al. 2011). Life history theory suggests that an increase in available food energy may be invested in elevated reproductive output, if investment in growth and defence does not change (Barnes and Partridge 2003). Given the degraded state of large predator populations throughout much of the wider Caribbean, the speed of the lionfish invasion may have been fuelled by a lack of predation, a lack of competition and, indeed, by a lack of fear.

Many questions remain to be answered about the remarkable success of the lionfish colonisation of the wider Caribbean. Our study represents what is, to our knowledge, the first use of stable isotopes in quantifying the trophic position of lionfish relative to an invaded community and how that position may change across habitats, with body size, and in response to predator abundance. We hope that the work may provide a useful baseline for the generation and testing of further hypotheses that will collectively provide a clearer understanding of how this relatively uncommon fish undertook such a consummate invasion.

Acknowledgments

The authors would like to extend their sincere gratitude to Iliana Chollett Ordaz for production of figures, Rona McGill for processing of samples and data quality checking, Mike Furlong for generous use of lab equipment, Rich Inger for helping with mixing models, and John Pinnegar for valuable advice during early stages of research. Fieldwork was supported by Cefas and the UK Natural Environment Research Council (NERC), who also funded sample processing at the NERC Life Sciences Mass Spectrometry Facility.

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6

General Discussion

The first research chapter (chapter two) of the thesis presented here examined the response of a number of herbivorous and predatory species to a ban on the use of fish traps in Bermuda. Perhaps the most surprising result was that there did not appear to be an increase in juvenile scarid abundance despite the fact that adult biomass increased by a factor of 2.67. The increase in adult scarid biomass correlated with an increase in the biomass of the trumpetfish, *Aulostomus maculatus*, which multiplied by a factor of 6.57 over the course of the nine-year study window. Because aulostomids are not fisheries targets in Bermuda (B. Luckhurst, pers. comm.) and are not retained as by-catch in traps (S. O'Farrell, pers. obs.), they would not be expected to have been suppressed by the trap fishery and would thus not experience a release from fishing pressure. However, aulostomids are voracious predators of juvenile fishes and a parsimonious explanation for our result is that the population explosion in aulostomids was fuelled by an increase in settling juveniles of scarids and perhaps many other species that the trapping ban released from fishing pressure.

However, 'correlation is not causation' and it is not possible to say with great confidence that our conjecture is correct. For example, the lack of response in the abundance of scarid juveniles could perhaps have been as a result of density-dependent processes in the planktonic phase, where predation may have increased commensurately with scarid larval abundance, although this hypothesis leaves unexplained the magnitude of the increase in aulostomid biomass. The argument for or against our most parsimonious explanation could perhaps be clarified by a 'before/after control impact' design field study that removed aulostomids from one of our three study sites whilst retaining them at the others. If pulses of settlers were being absorbed by aulostomid predation, we would expect to see juvenile abundance increase at the manipulated site but not at the control sites that retained high aulostomid biomass.

If the hypothesis were upheld that aulostomid predation could absorb increases in juvenile abundance, this would have implications for management interventions that aim to enhance fish populations, such as the installation of marine protected areas. Aulostomids do not generally attract much research interest, but they could turn out to be more important in coral reef fish ecology than has been thought up until now. Recruitment of reef fish fluctuates in time and space, and being generalist predators (Randall 1967), aulostomids may be capable of exploiting settlers from

whichever species is most abundant at any given time on any given reef. Such behaviour would serve to dampen population fluctuations of reef fishes but would mean that aulostomid abundance would remain relatively constant in population census data, masking the dynamism of the process. The particular nature of the situation in Bermuda where prey abundance may have increased dramatically and consistently over a number of years, but the abundance of predators on aulostomids remained relatively constant, may have afforded a rare insight into a process that occurs widely but is hard to detect.

There are a number of ways in which we could attempt to test whether equilibrium aulostomid populations dampen fluxes in reef fish recruitment. If the arrival of settlers from all reef fish species are clustered in time at a given reef (e.g., high recruitment during El Niño/La Niña events when winds drive larvae towards a given reef rather than away from it) we might expect a lagged response in aulostomid biomass, as described by Lotka-Volterra predator-prey cycles (Lotka 1925; Volterra 1926). Conversely, if settlement of different species varies independently in time, we may expect aulostomids to opportunistically switch diet on an annual basis, which could be elucidated by a stable isotope time series across an aulostomid's life (with appropriate replication), as can be obtained by sampling across a sectioned otolith, bone or other hard body part that continues to grow throughout the life of the fish.

The second research chapter of the thesis (chapter three) proposed a novel approach to modelling mortality in the scarid, *Sparisoma viride*. The model explicitly considers mortality as acting independently on the partially decoupled organismal traits of age and body size, as is the situation in nature where older or smaller individuals are more likely to die, the former owing to senescence and the latter owing to predation. This biologically informed modelling approach performed considerably better than the most widely used approach to modelling mortality in fishes, namely the coefficient of natural mortality, usually denoted by the letter M . It would be very interesting to apply the trait-dependent mortality modelling approach to other species commonly modelled using M , such as many fisheries species, and to determine whether stock management success could be improved if it switched from using the 'lowest-common-denominator' approach of applying equations generalised from 175 different fish stocks (Pauly 1980) to calculate a mortality coefficient that assumes all individuals in a population have an equal probability of mortality regardless of age or size, which decades of fish ecology have shown not to be the case.

Chapter four developed and tested a novel method for estimating von Bertalanffy somatic growth rates from mark recapture data when few samples are available. The approach was tested against

the most widely used current method, namely that of Fabens (1965). The novel method performed well on simulated data of an idealised species (based on a parrot fish), but two interesting and useful pieces of work that could follow on from the chapter would be to test the method on other idealised fish taxa to see how body size and growth trajectories may affect performance, and to test it on field data of actual fish. The advantage of using simulated data to test such techniques is that the ‘true’ parameter values are known accurately and precisely, whereas to test on field data is really to test the method against other methods (e.g., curve fitting to otolith data or maximum likelihood analysis of repeated measurements) rather than on other species, per se. However, where long term, rigorously compiled growth rate datasets exist, the exercise may prove fruitful.

The lionfish invasion on which chapter five focussed is a fascinating topic, and perhaps the most compelling question of all is how the invasion occurred so swiftly, given the relatively rarity of the fish in its home range. A number of hypotheses have been presented to date, mostly centred on the *enemy release hypothesis* (ERH, Keane and Crawley 2002) whereby an exotic species may experience a release from predation, resulting in enhanced survivorship. The ERH is intuitively appealing, and there are many anecdotal examples of speared lionfish successfully being fed to sharks, groupers (Serranidae), snappers (Lutjanidae), moray eels (Muraenidae) and lobsters (Palinuridae), amongst others. However, given the enormous regional interest in the lionfish invasion and the widespread fishing of Caribbean predators, there are very few reports of lionfish actually being found in gut contents. Although there are anecdotal reports of spiny lobsters attacking and eating lionfish in aquaria (see Gulf and Caribbean Fisheries Institute list-server for multiple threads) and on reefs (Bruce Purdy, pers. comm.), whether most Caribbean predators will consume lionfish without human intervention remains far from certain. However, as had been shown in other marine ecosystems, predators can control prey populations through channels other than direct consumption, and the ERH may be considered from many different angles.

Heithaus et al. (2008) contend that predators influence prey populations in two ways, by inflicting direct mortality (*lethal effects*) and by inducing population-level behavioural changes resulting from anti-predator responses (*risk effects*), and they argue that risk effects may sometimes be more influential than lethal effects. For example, they may manifest themselves over wider spatial scales (e.g., relocation of prey species to previously unexploited habitats), and they lack the compensatory mechanisms that partially ameliorate lethal effects, such as density-dependent responses, and increased resource availability for the surviving prey population.

Heithaus et al. (2008) go on to define risk effects as the quantity of resources that a consumer will forgo in order to avoid exposure to predation. In a study of predation by tiger sharks (*Galeocerdo cuvier*) on Australian dugongs (*Dugong dugon*), Wirsing et al. (2007) found that the prey animals adjusted their spatial distribution in accordance with seasonal changes in shark abundance. The study found that the herbivores preferentially foraged in high-productivity, shallow-water seagrass habitats when sharks were few, but foraged in deeper, lower-productivity habitats when shark numbers increased, and therefore that the presence of tiger sharks shifted grazing between habitats, cascading to influence the standing biomass of primary producers.

Whilst collecting lionfish fin clippings for the stable isotope analysis presented in the present thesis, the authors spent a good deal of time observing individuals. Although we did not gather behavioural data at the time, it was very notable how much more skittish the invaders were inside the Exuma Cays Land and Sea Park (ECLSP), where predator abundance is high. Outside the park, the fish were substantially bolder and divers could almost touch them with the point of a spear without provoking any reaction.

I hypothesise that the presence of predators within the ECLSP may be inducing risk effects in lionfish in the same way as tiger sharks do in dugongs, namely whereby the prey species does not forage as optimally as they would in the absence of the predator. I stress that such risk effects could occur even in the absence of direct predation on lionfish: the elaborate and metabolically-expensive defences of lionfish strongly support the hypothesis that they evolved in a regime of high predation, and it is likely that a lionfish will 'recognise' any predator, such as a grouper, as a threat even if a Caribbean grouper does not recognise an exotic lionfish as prey.

Given the very high investment in reproduction undertaken by lionfish (Morris et al. 2011), if such risk effects exist they may manifest themselves as a decrease in spawning output as foraging efficiency drops (Figure 6.1). Such an effect could partially explain the astonishing speed with which the lionfish have colonised the western Atlantic, where predator populations are generally lower than in the native range of lionfish, the reduction in risk driving elevated foraging efficiency for the invader.

In an attempt to answer this question, we set out collect lionfish ovaries from across the boundary of the ECLSP. The high biomass of predators inside the Park is more similar to many of the invader's native Indo Pacific reefs, and stand in stark contrast to the most of the modern Caribbean. Eggs are metabolically more costly to produce than sperm making any 'risk effect' more easily discernable

but, unfortunately, every one of the 14 lionfish we managed to collect inside the park turned out to be male. The odds of encountering such a sex skew by accident are 0.5^{13} , or 1 in 8192, and it would be interesting to know if the Park somehow skews lionfish sex ratios, or indeed, if there are sex-specific behavioural differences that skew the encounter probability with divers. One way or the other, however, whether risk effects impact on the reproductive potential of lionfish remains answered.

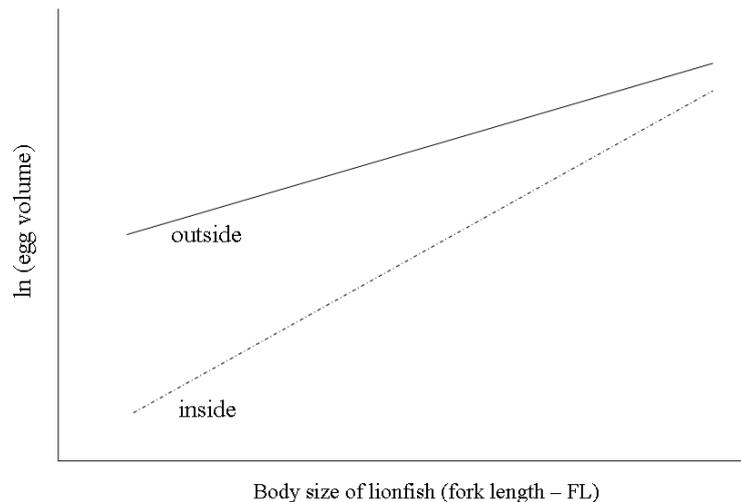


Figure 6.1 Schematic of the hypothesis that the presence of large predators inside the Exuma Cays Land and Sea Park may reduce lionfish foraging efficiency, impacting on investment in egg production. Risk-effect size may diminish with increasing fork length owing to size escape from predation, as indicated by the convergence of the lines.

Whether or not Caribbean predators will eat lionfish unbidden may be unresolved, but that lionfish will eat juvenile groupers is established, with Morris and Akins (2009) finding the remains of both Nassau grouper (*Epinephelus striatus*) and tiger grouper (*Serranus tigrinus*) in stomach contents. Given the voracious appetite for juvenile fish that has been documented in lionfish (Albins and Hixon 2008), it is possible that native predators in the Indo Pacific actually cultivate the fish assemblage to enhance the survival of their own juveniles by actively cropping down lionfish populations. Such cultivation/depensation effects (Walters and Kitchell 2001) may be common in fish communities, and have been demonstrated both in the North Sea (Fauchald 2010) and the Atlantic (Frank et al. 2011). Atlantic cod (*Gadus morhua*) prey on Atlantic herring (*Clupea harengus*) which in turn forage for cod eggs in the benthos. In an elegant example of ecosystem hysteresis (Holling 1973), cod crop down herring populations to reduce mortality on their own

young, arresting the system in a cod-dominated state. When overfishing decimated the cod, the herring population was released from predation and experienced a boom, dramatically enhancing mortality on cod eggs and reversing the predator-prey system whereby the foraging herring came to control the predatory cod (Fauchald 2010). A similar predator-prey reversal most likely contributed to the slow recovery of cod and haddock populations on the Scotian Shelf of Canada's east coast, and only now after two decades of a fishing moratorium are the top predators beginning to regain control of the system (Frank et al. 2011). The considerable investment in defensive mechanisms by lionfish implies that predation has had a profound effect on their evolutionary history, and the situation in the invaded Caribbean where lionfish are consuming vast numbers of juvenile predators and their prey items makes it easy to see how cropping of lionfish in the Indo Pacific would have elevated the fitness of native predators.

The final hypothesis I offer to explain the invasion success is simple but difficult to test. Caribbean lionfish produce enormous numbers of eggs (Morris et al. 2011) and it may be assumed that their Indo Pacific conspecifics do likewise. Over evolutionary timescales, such a constant supply of eggs may well have supported considerable populations of planktonic predators. The gelatinous matrix within which lionfish eggs are encased may be a defence against planktonic predation, resulting from an evolutionary "arms race" between predator and prey. The arrival of lionfish in the Caribbean may have released them from mortality in the plankton rather than on the reefs, and the absence of their specialised planktonic predator(s) may have underpinned the population explosion that has occurred.

Territoriality in *Sparisoma viride*

Many research avenues were considered before settling on the final content of the present thesis, and a number of alternative studies were thwarted by a lack of data or time. However, such topics may interest the reader as much as they do the author, and the general discussion presents the opportunity to consider a number of these ideas, focussed broadly on territoriality of stoplight parrotfish, *Sparisoma viride*.

The social organisation of stoplight parrotfish (*Sparisoma viride*, hereafter 'stoplights') is highly complex (vanRooij et al. 1996, and the General Introduction to the present thesis) and was very influential on the design of the population model presented in Chapter 3. Although only tangentially related to growth and mortality, the population structure of the species is of great interest, and represents an alternative route that the present thesis may have taken. Brightly-

coloured terminal phase males energetically guard territories close to the ‘drop-off’, at the interface between the reef structure and open water. These territorial terminal phase (TTP) males probably guard the territories to maximise mating success rather than access to food, a conjecture supported by the observations that all spawning takes place near the drop-off, chasing behaviour tends to increase in the spawning hours, and TTP males chase male conspecifics from their patch but not other species that share the same food resources (SOF, pers. comm.) such as the redband parrotfish, *Sparisoma aurofrenatum*.

Spawning near the drop-off allows gametes to be carried off into the water column where predator and parasite densities are generally lower than on the reef (Grutter et al. 2010), and the tacit paradigm is that males select and guard territories, into which females subsequently migrate in order to mate with the male as part of ‘his harem’. However, I hypothesise that this may not be the case, but rather that female spatial distribution is driven by other factors, and male territories are overlaid on this underlying pattern.

For a TTP male, guarding as large an area of reef that he can economically defend should increase his fitness, whether he is trying to attract more females to his larger territory, or simply hoping that by making his territory larger it will probabilistically contain more females whose distribution is controlled by other factors. For a female, however, there are no apparent barriers to movement among territories, and it is difficult to imagine a fitness benefit of mating exclusively with a single male. Stoplights are broadcast spawners so there is no parenting benefit, and I have neither seen nor heard of a TTP male defending a female against predation. Stoplights spawn daily and individual TTP males have been observed spawning up to 13 times a day (vanRooij et al. 1996) with multiple females in their territories. Given such capacity, females may be expected to best serve their fitness by mating with multiple males, rather than gambling their fitness on a single male of unknown genetic quality, yet females return to the same territories daily (vanRooij et al. 1996). Since it is hard to imagine a fitness benefit of remaining loyal to a specific TTP male, especially since females swiftly switch allegiance to a new TTP male when the incumbent dies (vanRooij et al. 1996), I hypothesise that females exhibit fidelity to a particular area of reef. The factors that make one area more attractive than another to a female may be driven by proximity to the reef crest, and by the spatial distribution of cleaning stations.

Herbivores survive on food that is low in nutritional content, especially protein (Mill et al. 2007). Parrotfishes produce very large numbers of gametes almost continuously, and anything that retards energy conversion must be highly undesirable, and especially so for females as eggs are

metabolically more costly to produce than sperm. Female stoplights at Glover's Atoll in Belize spend up to a quarter of their time being cleaned (SOF, unpubl. data.) which implies that the activity is highly non-trivial. The influence of parasites such as gnathiid isopods on coral reef fish ecology is probably underestimated and, as parasite abundance tends to scale with host body size (Grutter and Poulin 1998), larger and more fecund females may be driven to minimise their energy lost to parasitism and preferentially divert it towards egg production. In this scenario, male territories may be distributed according to female distribution, or simply maximised spatially to probabilistically contain as many females as possible. One way or the other, the so-called 'harem' may be a product of female fitness concerns as much as, if not more than, those of TTP males.

The growth and mortality of coral reef fishes on which the present thesis has touched is a highly complex topic about which there is a great deal left to understand. Advances in genetics and biophysical modelling of larval dispersal are providing increasingly sophisticated tools for those attempting to understand how reef fish metapopulations function, and to test hypothesis that were hitherto intractable owing to limitations in computing power. With reef fish populations dwindling throughout the world (Newton et al. 2007) as human populations burgeon and the demand for fish protein increases, capitalising on such advances will be essential if many of the oceans' fish populations are to persist in the centuries to come.

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