FACTORS AFFECTING POPULATION DYNAMICS OF THE ROUND GOBY

FACTORS AFFECTING POPULATION DYNAMICS OF THE INVASIVE ROUND GOBY (*NEOGOBIUS MELANOSTOMUS*)

By

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1 Preface

This thesis consists of two co-authored works, prepared for publication as Journal Articles. Individual contributions to these pieces are as follows.

Part I: Demography and substrate affinity of the round goby *Neogobius Melanostomus* in Hamilton Harbour. Data for this study was collected in the field by JAMY, JRM, JIM, SEMR, AV, CG and SB as indicated in the Methods section of the article. The data were analyzed by JAMY, under the supervision of DJDE and SB, with statistical advice from PDMM. All authors contributed to the writing of the article, with JAMY as the primary author of the Results section.

Part II: Modelling the population dynamics of male alternative reproductive tactics The mathematical model for this study was developed by JAMY, with assistance and supervision from DJDE and biological advice from SB. Model analyses were conducted by JAMY; Numerical work was conducted independently and analytical work was carried out with assistance from DJDE. The primary author of the article was JAMY, with contributions to the introduction from SB and editing by SB and DJDE.

Abstract

The round goby (*Neogobius melanostomus*) is an invasive fish species that has spread rapidly throughout the Great Lakes. The proliferation of this invasive species is of interest and concern because of its potentially negative impacts on native species. This thesis focuses on increasing our understanding of the population dynamics of the round goby, exploring causal factors both empirically and theoretically.

We analyzed data collected in Hamilton Harbour (in Lake Ontario) between 2002 and 2008. We found that round gobies have declined over time in both abundance and in body size. We related the observed dynamics to seasonality, to substrate types and to water quality in all locations. Round gobies were found on all substrates sampled including mud, although they were less abundant on mud than on other substrates, and to date have not extensively colonized Cootes Paradise Marsh, an important breeding ground for native fishes. Our results indicate that muddy and sandy substrates are not resistant to round goby invasion, and may impede but will not prevent round goby colonization.

Recently, two types of phenotypically distinct males have been observed in the population that have different strategies for reproducing. Through mathematical models, we investigate the affects of Male Alternative Reproductive Tactics on population dynamics. We compare two models in which we assume that tactics are inherited, or not inherited from the parent. We found in both cases that the presence of sneaker males can result in significantly increased populations, but can also suppress the population. When tactics are not inherited, the model predicts one of three scenarios: extinction, persistence, or persistence above a threshold density (Allee effect). When tactics are inherited we find four possible situations: extinction, a population consisting only of parentals, a coexistence equilibrium, or stable population cycles. Our results suggest that it is important to incorporate alternative reproductive tactics into population models, particularly for species of environmental or commercial concern.

2 Acknowledgements

Enormous thanks to my fantastic supervisors, David and Sigal, for your support, dedication, and exhaustive efforts. To Dr. Macdonald for enlightening chats about all things statistical. To Susan and Julie for the piles of references, and to the entire Balshine lab for help with presentations, and for making me feel more like a scientist. To everyone who caught fish, thanks for the data! To my friends for their endless supply of encouragement. To Katie and Shannon for logic and sanity checks at the chalkboard, and to John for Programming 101. To the professors of the Arts & Science program for a wonderful undergraduate experience. To Dr. Viveros for being a most excellent undergraduate thesis supervisor; I might not otherwise have pursued graduate research. To Nick for providing fishy supplies and quality break time. To my parents and sister for love, support, and helping me get this far.

So long, and thanks for all the fish.

Contents

List of Figures

3 Introduction

The round goby (*Neogobius melanostomus*) is an invasive fish species that has spread rapidly throughout the Great Lakes, including Hamilton Harbour in Lake Ontario (Balshine et al., 2005; Charlebois et al., 2001; Dillon and Stepien, 2001). This invasive species is of interest not only because of its rapid expansion, but also because it poses a threat to native species (Chotkowski and Marsden, 1999; French and Jude, 2001; Janssen and Jude, 2001; Kuhns and Berg, 1999; Steinhart et al., 2004). Understanding what factors affect changes in populations over time is an important step in building a conservation strategy or a invasive species eradication plan. This thesis addresses the population dynamics of the round goby, exploring causal factors both empirically and theoretically.

Part I of the thesis assesses the population changes of round gobies in Hamilton Harbour using data collected between 2002 and 2008. We observed reductions in the abundance of round gobies over time, as well as in their body size and condition. We assess the impact of various factors on these measurements, such as season, water temperature, and substrate (or habitat) type. Of these factors, the effects of substrate on abundance are of particular concern, because of Hamilton Harbour's connection to Cootes Paradise Marsh, a wetland that serves as in important spawning ground for warm water fishes (Holmes, 1988). Substrate preference could influence the expansion of the round goby into this and other wetlands, as well as in the Great Lakes and their many tributaries in general.

Another factor that may influence population characteristics is the presence of more than one type of male in the population. Recently, alternative male reproductive tactics have been observed in round gobies (Marentette et al., 2009); larger males build nests, court females and guard the eggs while smaller males will simply sneak in to fertilize these eggs without courtship, nest defence or egg care. Sneaker males essentially exploit the efforts of the parental males (Oliveira et al., 2008). Part II of the thesis explores the theoretical impacts of these two alternative male reproductive tactics on population dynamics using mathematical models. We discuss the different dynamics that can be observed, and the associated conditions required for such behaviour. We also assess how changes in model parameter values affect the population size as predicted by the model.

Submitted for publication in the Journal of Great Lakes Research

Demography and Substrate Affinity of the Round Goby (*Neogobius melanostomus*) in Hamilton Harbour

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Abstract

The invasive round goby, *Neogobius melanostomus*, consumes eggs and fry of other fishes, competes for resources with native fish species, and hence poses a threat to Great Lakes aquatic communities. We provide the first description of round goby demographic patterns in Hamilton Harbour, in the western tip of Lake Ontario, and the connected Cootes Paradise Marsh, a wetland under restoration. By monitoring round goby populations on a variety of distinct habitats for seven years (2002-2008), we found that populations have declined at all sample locations and that average fish body size also has decreased. We also related abundance, body size, and reproductive patterns to seasonality, to substrate types (mud, sand, cobble and boulder) and to water quality in all locations. Round gobies were found on all substrates sampled including mud, although they were less abundant on mud than on other substrates, and to date have not extensively colonized Cootes Paradise Marsh. Our work confirms previous studies, which have suggested that habitats lacking hard structures will have fewer round gobies because they lack substrates on which round gobies can breed. However, our results also indicate that muddy and sandy substrates are not resistant to round goby invasion and will not prevent round goby colonization, a potential concern for Cootes Paradise Marsh, an important spawning, nursery and refuge habitat for warm water native fishes, and for other similar wetlands.

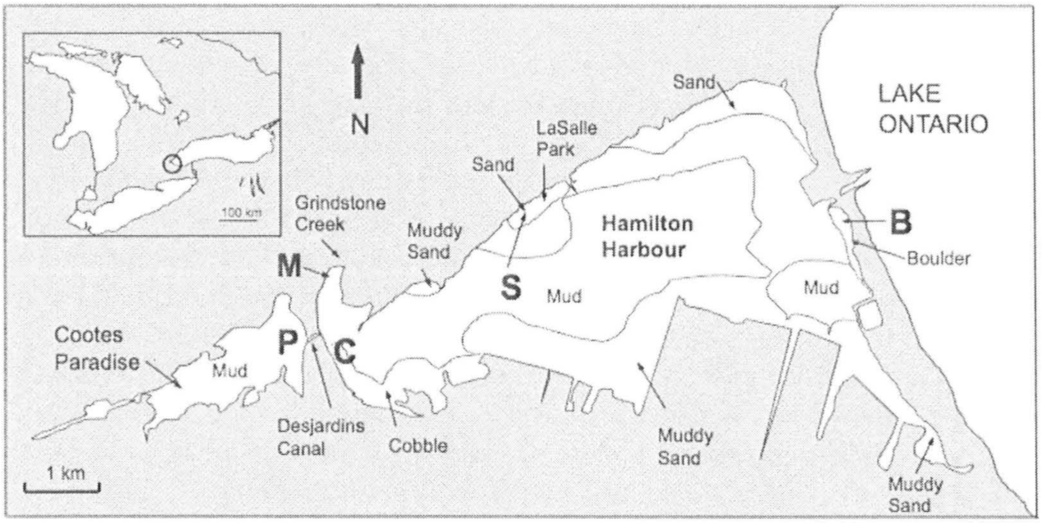

Figure 1: A map of Hamilton Harbour (43 °N, 79 °W) with the sampling locations and substrate types indicated. M refers to sites sampled with mud substrate, S refers to sites sampled with sand substrates, C refers to sites that were sampled with cobble substrates, B to sites with boulder substrates, and P refers to sampling sites in Cootes Paradise Marsh.

1 Introduction

Round gobies are native to the Black and Caspian Seas (Berg, 1949) and were accidentally introduced to North America via ballast water in the early 1990s (Jude et al., 1992). They have subsequently spread to all five of the Great Lakes faster than any previously introduced fish species (Charlebois et al., 2001; Dillon and Stepien, 2001). Round gobies were first detected in Lake Ontario in 1998 (Mills et al., 2003) and by June 2002 they were one of the most frequently caught species in the littoral zone in Hamilton Harbour (Balshine et al., 2005).

The abundance of round gobies in Hamilton Harbour is of particular concern because the harbour is attached by a narrow man-made channel, Desjardins Canal, to Cootes Paradise Marsh, a large wetland and important breeding ground for native fishes in Lake Ontario (Fig. 1; Holmes, 1988; Lougheed et al., 2004). Cootes Paradise was previously one of the most degraded areas in the Great Lakes (Holmes, 1988), but ongoing restoration (such as extensive planting of native species, and the construction of a fishway/barrier to exclude common carp, *Cyprinus carpio*) has improved the physical habitat and stemmed the decline of native species such as yellow perch, *Perca flavescens* (Brousseau and Randall, 2008; Holmes, 1988). Previous research has shown that round gobies can negatively impact other species of fish in part by eating their eggs and young (Chotkowski and Marsden, 1999; French and Jude, 2001; Steinhart et al., 2004a). As well, several studies have shown that, as round gobies have increased in density, other species such as mottled sculpin, *Cottus bairdii* (Janssen and Jude, 2001) and caddisfly, *Oecetis* spp. (*Trichoptera*; Kuhns and Berg, 1999) have declined. In recent years, in an effort to improve conditions so that Hamilton Harbour might be delisted as an Area of Concern (International Joint Commission, 1999), a fisheries management plan (Bowlby et al., 2009) has been created to help support a sustainable and productive fish community. Large round goby populations in Hamilton Harbour and Cootes Paradise Marsh could compromise native fish breeding success as well as the goals of the Hamilton Harbour Remedial Action Plan (RAP; Hall et al., 2006) and other restoration efforts.

In both their native and introduced habitats round gobies have been found on many different substrate types including rock, coarse gravel, sand, on shell beds and among macrophytes (Clapp et al., 2001; Jude and DeBoe, 1996; Miller, 1986). A number of studies suggest that round gobies prefer structurally complex, hard, rocky habitats, with ample shelter for breeding (Miller, 1986; Vanderploeg et al., 2002). In Lakes Michigan and Erie adult round gobies were most abundant on rock while juvenile round gobies were found to be more abundant on sandy substrates, and it has been argued that adult round gobies will displace juveniles from favored, structurally complex habitats onto open, sandy substrates (Charlebois et al., 1997; Ray and Corkum, 2001). However, a recent study, near Pelee Island, Lake Erie, found round gobies to be as abundant on mud as on rock (Johnson et al., 2005). To date, explicit laboratory tests for substrate preference have not been conducted, but such preferences, or lack thereof, could influence the speed and success of the round goby range expansion.

The aims of this study were threefold. 1) To track changes in the abundance of the round goby in Hamilton Harbour over the course of its Lake Ontario invasion (2002-2008). 2) To compare abundance across four different substrate types: mud, sand, cobble, and boulder. 3) To examine how the body size of round gobies varied over time and season, and across the various substrate types. As our study began not long after the round goby was first detected in Hamilton Harbour (in 1999; OMNR, 2000), we hypothesized that round goby populations would initially increase and then eventually stabilize as they reached saturation (Begon et al., 1996). We also considered the possibility that populations might even decline as predators adapted to the presence of a new food source (Jaksic, 1998; Reusch, 1998). We also hypothesized that round gobies would prefer, and be most common on, hard, complex substrates on which they could deposit and guard eggs (e.g., boulder and cobble) and where they could best hide from predators. Finally, we hypothesized that these hard substrate habitats would harbour the largest round gobies, as these individuals could exclude smaller round gobies from preferred sites (Ray and Corkum, 2001).

2 Methods

2.1 Demography and Habitat Affinity

Round gobies in Hamilton Harbour were sampled from 2002 to 2008 and collected at least twice each month from May to October, with the exception of 2003 when sampling occurred only once each month. In all seven years we used baited minnow traps set out at four sites around Hamilton Harbour. Each site represented a different substrate type: mud, sand, cobble and boulder (Fig. 1), defined by particle size following the substrate scale proposed by Krumbein and Sloss (1951). Substrate was measured using either a measuring tape (cobble, boulder), or a stage micrometer on a dissecting microscope (mud, sand). Boulders (N=10) were on average 137 cm long, 127 cm wide and 48 cm high. The average size of the cobble (N=10) was 19.6 cm (length) x 14.2 cm (width) x 10.1 cm (height). Sand grains (N=20) were on average 733 m in diameter, and mud particles (N=8) measured on average 29 m in diameter. The sampling sites used were identical from year to year. At each site, two (2002-2004) or four (2005-2008) minnow traps, baited with approximately 25 g of frozen corn, were placed on the benthos 8-9 m from the shore, in water 60 to 100-cm deep. Although some mark recapture studies have reported capturing gobies up to 67 m from the initial point of tagging (Wolfe and Marsden, 1998), one study that specifically addressed high site fidelity in round gobies reported a minimum home range of approximately 5 m^2 (Ray and Corkum, 2001). Based on the information from this latter study, traps were placed at least 10m apart. All fish captured in each trap were collected 24-hr later. Additionally, traps (two in 2003-2004 and eight in 2005-2007) were placed in Cootes Paradise Marsh (at the eastern end of the marsh closest to the mouth of the Desjardins Canal; see Fig. 1). Water quality was assessed at each site and on each sampling occasion (2004-2008) by monitoring water temperature, dissolved oxygen, pH (with a YSI 550A field meter) and water clarity (using a Secchi disk).

All round gobies caught were counted, sexed and measured. The sex of each fish was determined by visually examining the urogenital papilla between the anus and the base of the anal fin (Miller, 1984). Fish that could not be sexed were recorded as juveniles. The standard lengths of the fish were measured to the nearest mm. Body mass was measured by drying the fish with a towel and placing it on a portable digital balance, accurate to 0.1 g. Body condition was determined using Fultons body condition index (10^5x[body mass (g) / standard length (mm)^3]; Ricker, 1975). Gonad mass was measured from 2004-2008, and the Gonadosomatic Index (GSI) was calculated (100 x [gonad mass (g)] / [body mass (g) gonad mass (g)]; Schreck and Moyle, 1990). Fish were considered to be in reproductive condition if their GSI exceeded 8 % (for females) or 1 % (for males), as these represent minimum GSI values found for reproductive round gobies in other studies (Gammon et al., 2005; MacInnis, 1997; Marentette and Corkum, 2008).

2.2 Statistical Analyses

Statistical tests were performed using the statistical programming language R, version 2.7.1. Data were checked for normality, transformed whenever necessary and parametric statistics were used whenever possible, i.e., where assumptions for parametric tests (normality and sample homoscedasticity) were met. Standard length data was log-transformed and body mass was transformed with log(mass+1). Males and females were compared using χ^2 tests for abundance statistics, *t*-tests for standard length and body mass, and Mann Whitney *U* tests for body condition. Abundance (count) data was fit to a quasi-poisson general linear model (GLM), and percent data to a binomial GLM (logistic regression; Fox, 2002, pg 155-190, Agresti, 2002). Type II, 3-factor ANOVAs were performed on all parametric statistics using the R-package "car"; Fox, 2008) with year, site, and month as factors. Type II ANOVAs are preferable to use when there is an unbalanced design. They test the significance of each term in the model after all others, except for the term's "higher-order relatives" or related interaction terms (i.e. they follow the principle of marginality; Fox, 2008). Multiple all-pair post hoc comparisons were performed using the R-package "multcomp" (Hothorn et al., 2008) with Bonferroni corrections for multiple comparisons. Kruskal Wallis tests were used for body condition, GSI, water temperature and clarity data (as these could not be normalized) and these tests were followed by multiple comparison between treatments (Siegel and Castellan, 1988, pg 213). All tests were two-sided, and were considered significant at p-values less than or equal to 0.05.

To account for sampling irregularities such as trap theft, drift or breakage, fish per trap was used as the measurement of abundance. The traps were placed in identical locations each week and each year for the abundance study. Occasionally, extra traps were set at the four sites (away from the abundance study traps) to collect fish for experiments. These fish were excluded from the abundance counts, but were measured and included in analysis of morphological data. Hence the sample sizes for body characteristics and abundance were not identical.

3 Results

3.1 Patterns Across Years

Over the seven years of study, a total of 4617 round gobies were caught in Hamilton Harbour. There was a 72% decline in mean fish per trap between 2002 and 2008, and this decline was linear (Fig. 2a, Table 1; 3-factor ANOVA, overall model: $F_{77,1022} = 7.0$, $p < 0.0001$; effect of year: $F_{6,1022} = 30.2$, $p < 0.0001$; linear trend analysis on year: $F_{1,1093} = 135.5$, $p < 0.0001$; see Maxwell and Delaney, 2004, pg 243-274 for further statistical details on linear trend analyses).

Of the fish caught, 4403 could be sexed. The remaining 214 fish were sexually immature and recorded as juveniles. Many more males ($n_{\text{males}} = 2979$) were caught than females (Fig. 2a; $n_{\text{females}} = 1424$, chi square test: $\chi^2 = 549.2$, $df = 1$, $p < 0.0001$), giving an overall sex ratio of approximately two males for every female. Indeed 71% of the catches were male-biased (of a possible 396 sampling occasions, 280 resulted in a male-biased catch, where an occasion includes all fish caught at one site on a given day, $\chi^2 = 67.9$, $df = 1$, $p < 0.001$). Despite the overall decline in fish numbers, the sex ratio (number of male fish/female fish) remained strongly male biased and

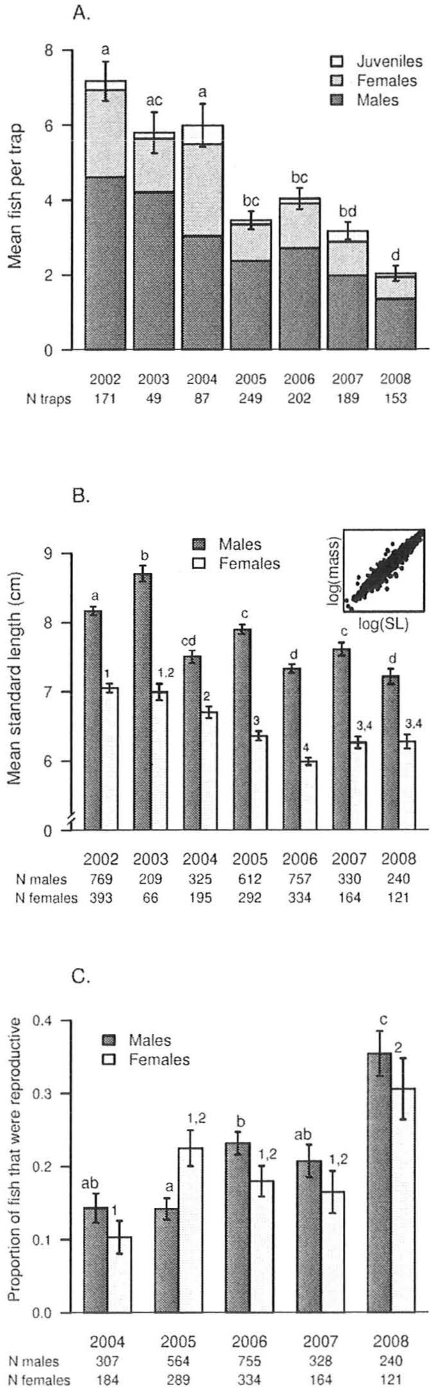

Figure 2: **(a)** Mean number (±SE) of round gobies / trap by year of collection, all four substrates combined. Juveniles could not be sexed, and so are included in abundance figures only. Letters atop the bars show statistical significance; bars that do not have a letter in common differ significantly at $p < 0.05$ (based on multiple all-pair post hoc comparisons with Bonferroni corrections). **(b)** Mean (±SE) standard length in cm of both males and females by year of collection, with all four substrates combined. Means shown have been reverse-transformed to show original body lengths. Statistical significance is denoted as in Fig 2a, using letters for males and numbers for females. Inset: The relationship between fish standard body length and body mass (log transformed). **(c)** The proportion of fish (±SE) that were reproductive in each year of collection. Fish were considered reproductive if their GSI exceeded 1% (males) or 8% (females). Statistical significance is denoted as in Fig 2a.

Table 1: Mean fish caught per trap by year and substrate type.

Substrate	2002	2003	2004	2005	2006	2007	2008
Mud	4.2	3.3	5.8	1.5	1.7	0.9	0.5
Sand	6.3	6.3	3.9	4.8	5.8	3.9	2.8
Cobble	8.2	4.9	6.8	4.1	4.9	4.1	3.1
Boulder	9.7	7.7	7.5	3.9	3.8	3.6	1.8

relatively constant over time apart from one year (2004) when the male bias was less extreme (Fig. 2a; test for constant proportion across years: $\chi^2_{2004} = 5.5$, $df = 1$, $p = 0.02$; χ^2 for all other years > 47.0, $p < 0.0001$).

Round gobies caught in Hamilton Harbour averaged 74.4 ± 0.2 mm [mean ± SE] in standard length (range 31-132 mm) and 12.0 ± 0.1 g in body mass (range 0.6 to 64.8 g). Overall, males were longer, heavier and in better condition than females (Table 2; two-sample t-tests: standard length, $t = 28.9$, $df = 1$, $p < 0.0001$; body mass, $t = 30.1$, $df = 1$, $p < 0.0001$; body condition, $t = 5.2$, $df = 1$, $p < 0.0001$). Body mass and length were highly correlated (Fig. 2b, inset; linear regression: $R^2 = 0.96$, $p < 0.0001$). The decline in overall round goby abundance was mirrored by a decline in body size; there was a 10% decrease in standard length and a 16% reduction in body mass between 2002 and 2008 (Table 2, Fig. 2b, standard length shown; effect of year, male standard length: $F_{6,3164} = 36.2$, $p < 0.0001$; female standard length: $F_{6,1487} = 37.9$, $p < 0.0001$). The downward trend in body size was confirmed in both males and females by a linear regression (standard length and body mass versus year of capture, $p < 0.001$ for males and females). While body size and abundance of round gobies decreased over time, the proportion of reproductive fish was higher in 2008 than in 2004 (Fig. 2c; 3-factor ANOVA with data fit to a binomial GLM, testing for constant reproductive proportions across years, for males: $n = 2195$: $\chi^2 = 31.8$, $df = 4$, $p < 0.0001$; for females: $n = 1094$: $\chi^2 = 12.8$, $df = 4$, $p = 0.01$).

3.2 Patterns Across the Breeding Season

Round goby abundance did not differ across the months that were sampled (Fig 3a inset; effect of month: $F_{5,1022} = 1.1$, $p = 0.38$). Temperature, however, was significantly related to fish abundance (Fig. 3a; effect of temperature, controlled for year, site, month: $F_{1,829} = 4.2$, $p = 0.04$), with the highest catch rates in waters between 15 and 17 °C. A strong seasonal pattern was observed in body condition; fish of both sexes tended to be lightest and in poorest condition just after the peak of the breeding season (June-August), and were heaviest and in the best condition early in the season (May) as well as late in the season in September/October (Fig. 3b; male body condition: Kruskal Wallis test, $H = 239.0$, $n = 3241$, $p < 0.0001$; female body condition: $H = 130.7$, $n = 1564$, $p < 0.0001$). There were also seasonal changes in reproductive patterns; the proportion of reproductive fish (males and females) decreased steadily from May to September, increasing again slightly in October in males (Fig. 3c; testing for constant reproductive proportions across month, data fit to a binomial GLM, for males: $\chi^2 = 426.3$, $df = 5$, $p < 0.0001$; for females: $\chi^2 = 218.3$, $df = 5$, $p < 0.0001$).

3.3 Patterns Across Substrate Types

Fewer round gobies were captured on mud than on boulder, cobble or sand, (Fig. 4a; effect of substrate: $F_{3,1022} = 41.8$, $p < 0.0001$). The observed decline in round goby abundance occurred on all substrates in Hamilton Harbour with the smallest decline on sand, and the largest decline on boulder (Table 1). In total, 199 round gobies were caught in Cootes Paradise Marsh, and the average number of fish/trap (0.8 ± 0.1, mean±SE) was significantly lower than the average number of fish/trap (2.0 ± 0.2, mean±SE) caught on mud habitats within Hamilton Harbour (Fig. 4a; Mann Whitney U test: $W = 42650$, $p < 0.0001$). Furthermore, most fish caught in the marsh were found in traps near the mouth of the canal leading to the harbour.

The overall population male sex bias was apparent on sand, cobble and boulder habitats. On these substrates, at least two males were caught for every one female (Fig. 4a; $df = 1$, all χ^2 values > 159.6, and all p values < 0.0001). On mud too, more males than females were caught but the bias

Table 2: Mean body measurements by year and by gender; standard length (SL) and body mass.

Body Measurement		2002	2003	2004	2005	2006	2007	2008
SL (cm)	Males	8.2	8.7	7.5	7.9	7.3	7.6	7.2
	Females	7.1	7.0	6.7	6.4	6.0	6.3	6.3
Mass (g)	Males	12.6	16.1	11.3	12.7	10.5	10.9	10.1
	Females	7.9	8.6	7.9	6.3	5.6	6.0	6.4

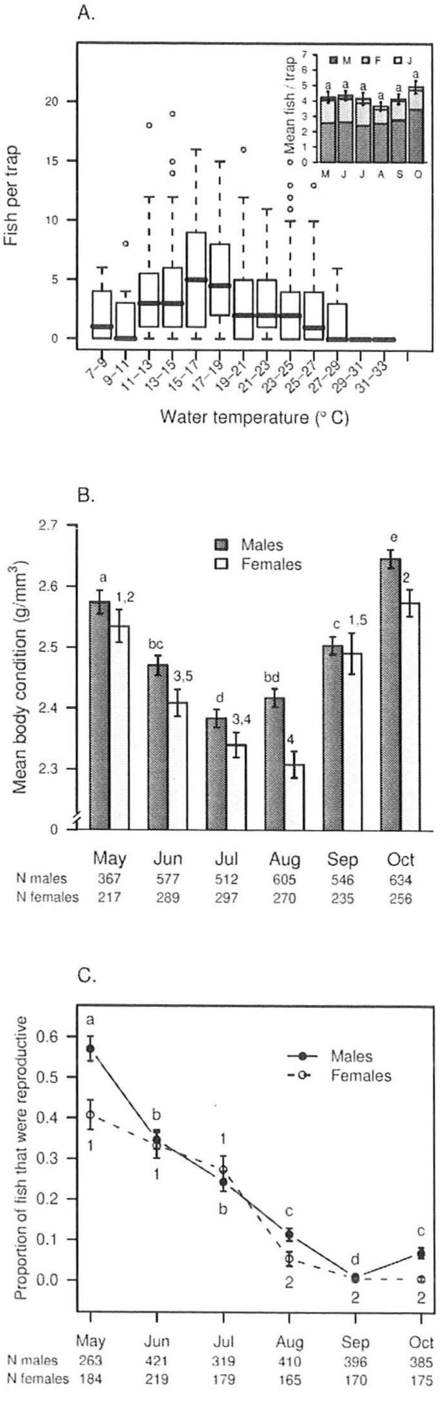

Figure 3: **(a)** Boxplots of number of round gobies caught in each trap by water temperature at time of collection. Boxes show medians and 25th/75th percentile. Dashed lines extend to the most extreme data point which falls within 1.5 times the interquartile range. Outliers (values beyond this range) are shown with open circles. Temperatures are binned into 2-degree intervals (ex. (7–9], (9–11], etc.) Temperature was related to abundance ($R^2 = 0.026$, $F = 22.14$, $p < 0.0001$), and including the term (temperature)^2 significantly improved the fit ($R^2 = 0.055$; comparison of models: $F = 25.9$, $p < 0.0001$), suggesting a quadratic (parabolic) function relates temperature to catch rate. **Inset:** mean number (±SE) of round gobies / trap by month of collection, years and substrates combined. Statistical significance is denoted as in Fig 2. **(b)** Mean (±SE) fish body condition (Fultons Index: 10^5x[g/mm3]) by month of collection. Means shown have been reverse-transformed to show values in the original scale. Males differed from females in condition in June ($p = 0.03$), August ($p < 0.0001$), and October ($p = 0.007$). Statistical significance is denoted as in Fig 2.**(c)** Proportion of all fish that were reproductive (when GSI exceeded 1% for males or 8% for females) in each month of collection.

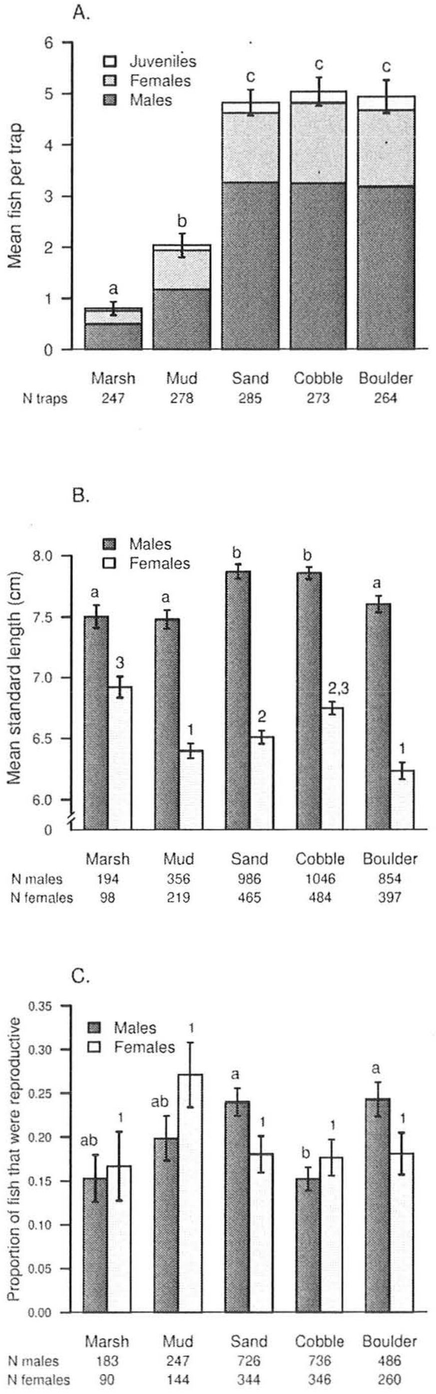

Figure 4: **(a)** Mean (±SE) number of round gobies per trap caught on various substrates in Hamilton Harbour and Cootes Paradise Marsh. Statistical significance is denoted as in Fig 2. **(b)** Mean (±SE) standard length in cm of males and female round gobies across substrate types. Statistical significance is denoted as in Fig 2 (with Kruskal-Wallis multiple post-hoc comparison). The picture is similar for both mass and body condition. **(c)** Proportion of fish that were reproductive (when GSI exceeded 1% for males or 8% for females) by substrate type. Statistical significance is denoted as in Fig 2.

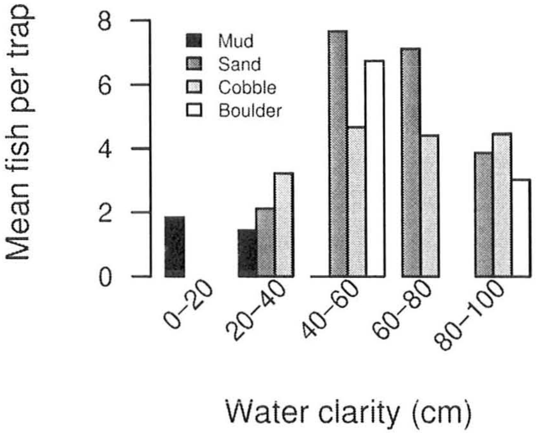

Figure 5: Mean number of round gobies per trap by substrate and clarity of water (in cm) at time of collection, as measured using a Secchi disk.

was less extreme (1.5 males to every female caught: $\chi^2 = 22.4$, $df = 1$, $p < 0.0001$). In Cootes Paradise Marsh, for every female caught there were 1.9 males caught ($\chi^2 = 18.6$, $df = 1$, $p < 0.0001$).

Fish captured on mud and boulders in Hamilton Harbour were smaller, lighter and in worse body condition compared to fish from sand and cobble (Fig. 4b, standard length shown; effect of substrate: male standard length $F_{3,3164} = 16.5$, $p < 0.0001$; male body mass $F_{3,3166} = 18.5$, $p < 0.0001$; male body condition, Kruskal Wallis test: $H = 73.6$, $n = 3241$, $p < 0.0001$; female standard length: $F_{3,1487} = 19.5$, $p < 0.0001$; female body mass: $F_{3,1488} = 20.2$, $p < 0.0001$; female body condition: $H = 24.0$, $n = 1563$, $p < 0.0001$). Interestingly, female round gobies caught in Cootes Paradise Marsh were some of the largest and heaviest females caught (Fig. 4b). Conversely, male round gobies caught from Cootes Paradise Marsh were among the smallest and lightest males caught. The proportion of females that were reproductive did not vary across substrates (Fig. 4c; testing for constant reproductive proportion across substrate, binomial GLM: $\chi^2 = 6.56$, $df = 4$, $p = 0.16$) but a higher proportion of males were found to be reproductive on boulder and sand compared with cobble ($\chi^2 = 20.4$, $df = 4$, $p < 0.001$).

Water temperature, pH and dissolved oxygen levels did not differ between substrates/locations (data pooled across years; temperature: Kruskal Wallis test, $H = 7.3$, $df = 3$, $n = 320$, $p = 0.06$; dissolved oxygen: $F_{3,166} = 0.89$, $p = 0.45$; pH: $F_{3,94} = 1.1$, $p = 0.36$). Water clarity, however, did vary across sites (Fig. 5; Kruskal Wallis test, $H = 185.6$, $n = 310$, $p < 0.0001$); it was least clear on mud and clearest on sand and boulder. Temperature correlated with fish abundance (Fig. 3a), but neither pH nor dissolved oxygen explained the variance in fish abundance (pH: $R^2 < 0.0001$, $F_{1,308} = 0.01$, $p = 0.91$; dissolved oxygen: $R^2 = 0.006$, $F_{1,564} = 3.3$, $p = 0.07$). Substrate type and water clarity both related to abundance (in a collinear manner) but the effect of substrate was much stronger (Fig. 5; effect of clarity alone: $R^2 = 0.086$, $F_{1,718} = 67.2$, $p < 0.0001$; effect of clarity after controlling for other factors: $F_{1,692} = 1.6$, $p = 0.21$; effect of substrate after controlling for other factors: $F_{3,715} = 16.3$, $p < 0.0001$).

4 Discussion

Between 2002 and 2008, round gobies in Hamilton Harbour decreased in terms of their abundance and body size. The significant decline in abundance occurred on all substrates. Conversely, investment in reproduction has increased over time. Round goby abundance in the near shore was related to temperature with the highest catch rate observed at water temperatures between 15 and 17 °C. In Hamilton Harbour, round gobies were least abundant on mud, and even fewer were caught in Cootes Paradise Marsh.

4.1 Population Decline

Our initial hypothesis of a population increase followed by a period of stabilization, was not met. The tandem declines in abundance and body size suggest that the round goby population in Hamilton Harbour may have reached, or even exceeded, its maximum carrying capacity prior to 2005. Our observations of decline may also represent an overshoot of carrying capacity, which may eventually settle to a stable level in coming years. Other fish species have recently increased in Hamilton Harbour (Brousseau and Randall, 2008), suggesting that the observed decline in round goby numbers is not merely a reflection of region-wide declines in fish abundance.

Factors such as predation or food supply may have influenced the abundance trends across years and it is possible that these factors might even select for earlier maturation or reduced growth. Aging studies are currently underway to test this suggestion. Studies have shown that predators such as smallmouth bass (*Micropterus dolomieu*), double-crested cormorants (*Phalacrocorax auritus*) and water snakes (*Nerodia sipedon insularum*) have begun to consume round gobies (King et al., 2006; Somers et al., 2003; Steinhart et al., 2004b). The strongest declines in round goby abundance were observed on boulders near a large colony of waterbirds (e.g. double-crested cormorants, Caspian terns, *Hydroprogne caspia*, ring-billed gulls, *Larus delawarensis*, and herring gulls, *Larus argentatus*). It is possible that prior to 2005 round gobies were more successful at escaping predation, but that in recent years potential predators have learned to recognize them as a new available diet item. Alternatively, the round goby decline may have more to do with the recent decline of zebra muscles (*Dreissena polymorpha*, a major diet item for round gobies) in Hamilton Harbour and in other areas of the Great Lakes (Charlebois et al., 1997; Petri and Knapton, 1999). To determine whether predation and food availability are contributing to the decline of round gobies, and to explore any compensatory responses in growth, fecundity and timing of sexual maturity, additional experimental studies (manipulating the presence of predators and diet restrictions) are now needed. It should also be noted that our own harvest of 4617 round gobies may have in part contributed to the observed decline of round gobies in Hamilton Harbour.

We used only minnow traps for this study, which may have led to some sampling bias. Capture in a minnow trap requires that fish actively explore the trap to be caught. Previous studies have suggested that minnow traps have a low catch rate compared to other sampling methods (Johnson et al., 2005). As a result, while our study can be used as a comparison of relative abundance across years and substrates, our catch rate is likely an underestimate of the true density of round gobies in Hamilton Harbour and Cootes Paradise Marsh. Only one sampling method (minnow traps) was used in this study, however pilot work has shown that this sampling method yields similar numbers to electrofishing and higher numbers than seining. Also, these other sampling methods were not equally successful on all substrates (electrofishing had poor yields on mud, and seining is not possible on boulder or cobble). Finally, temperature was more strongly related to abundance than was month of year, and may influence round goby catchability. Round gobies may reduce general activity in very warm or very cold waters, making them less likely to explore, forage and swim into a trap. Alternatively, our results could reflect a true preference for intermediate temperatures, with round gobies frequenting deeper waters (> 1 m) when temperatures are more extreme.

4.2 Male Bias

The strong male bias observed in this study and reported by Corkum et al. (2004) may be related to male round goby territoriality and paternal care. Like other goby species, only males defend a territory and care for eggs by fanning and defending the eggs (Corkum et al., 1998; Kangas and Lindstrm, 2001; Kvarnemo and Forsgren, 2000; Marentette et al., 2009; Miller, 1984). Males, therefore, will occupy the nesting areas in the shallow littoral zone for much longer (days and weeks rather than hours) than visiting females. Females may enter the shallow breeding sites only briefly to deposit eggs, remaining mainly in deeper water to avoid predation (Kovtun, 1979). Indeed, the male bias was less extreme during the peak of the breeding season, suggesting females migrate to deeper waters earlier than males (Fig. 3a). Although a territorial guarding male may have somewhat restricted movement compared to a non-reproductive male or a female, such males are more likely to interact with the trap near their nests as they are in these areas for longer periods.

Another explanation for the male bias may be because male round gobies are generally more active and explorative in the laboratory than are females (JR Marentette, unpublished data). Interestingly, pilot work using different fish sampling techniques (see Balshine et al., 2005) revealed a similar male-biased catch of round gobies. Male territoriality, exploration and paternal behaviours all may work together to make males more likely to enter minnow traps compared to females (see Balshine-Earn, 1996, for similar results for African cichlids).

4.3 Implications for Cootes Paradise Marsh and Other Wetlands

Our study suggests that mud alone will not exclude round gobies from wetlands/marshes like Cootes Paradise. Hamilton Harbour has been extensively colonized by round gobies (Balshine et al., 2005), including areas with muddy substrates previously thought to be devoid of round gobies. Although previous studies found that round gobies prefer structurally complex environments with many refuges and nesting sites (Miller, 1986; Ray and Corkum, 2001; Wickett and Corkum, 1998; Cooper et al., 2007), we found that round gobies had successfully colonized muddy substrates. In western Lake Erie Johnson et al. (2005) found round gobies on mud near Pelee Island, and they were even more abundant on mud than on sand. Soft substrates may actually provide effective hiding places from predators as round gobies can bury themselves (Jude et al., 1992). Furthermore, any lack of shelter on muddy substrates may be partially compensated for by more turbid waters reducing the effectiveness of predators that rely on visual or auditory detection (Jude and Pappas, 1992).

In our study, many fewer round gobies were found on mud and fewer still were found in nearby Cootes Paradise Marsh. One possible explanation for the much lower numbers in the marsh is that round gobies may have to migrate to seek refuge in tributaries or back into the Harbour when much of the shallow water column in the marsh freezes each winter (Bowen and Theysmeyer, 1998). The average depth in the Cootes Paradise Marsh is only 0.7 m and the maximum depth is 2 m (Chow-Fraser, 1999; Holmes, 1988). When the water levels in the marsh drop during the winter months, the majority of the fish communities are forced to migrate to deeper and warmer areas of Hamilton Harbour (Chow-Fraser, 1999). This need to repeatedly re-invade the marsh each year may have prevented the same scale of establishment as in the harbour. In Lake Michigan, Cooper et al. (2007) found fewer round gobies in wetlands than in adjacent lake habitats, and argued that wetlands may therefore act as barriers to invasion. Two other studies have suggested that wetlands might be barriers to round gobies as a result of their rich species diversity (Carman et al., 2006; Jude et al., 2006) The numbers of round gobies found on muddy habitats in Hamilton Harbour suggest that the muddy substrates of wetlands such as Cootes Paradise will not provide a barrier to invasion, but may slow down the rate of colonization and establishment.

Cootes Paradise is the largest and most important warmwater native fish breeding ground in western Lake Ontario (Holmes, 1988). If the round goby does manage to colonize Cootes Paradise Marsh, this could impact current restoration efforts. The round gobys generalized invertebrate feeding niche means that major impacts on the basal foodweb structure would be unavoidable. In some areas, native fish species have indeed declined where round gobies have become abundant (Crossman et al., 1992; Janssen and Jude, 2001). If round gobies invade the marsh in large numbers, native fish species will have to compete with round gobies for food (French and Jude, 2001), shelter and breeding habitat (Balshine et al., 2005). In addition, round gobies have been known to disrupt spawning and decrease reproductive success of native species by eating their young (Steinhart et al., 2004a). Species particularly at risk include sticklebacks (*Gasterosteidae*), darters (*Etheostoma* spp., *Ammocrypta* spp.), and logperch, (*Percina caprodes*; Balshine et al., 2005; Chotkowski and Marsden, 1999; Janssen and Jude, 2001).

This longitudinal study traced population dynamics of an invasive fish species, the round goby, in Hamilton Harbour and began at a presumed early time point in the round goby invasion of Lake Ontario. We have shown that the population appears to be declining in Hamilton Harbour. Nevertheless, the high densities of round gobies, their prolific reproduction and tolerance to a wide range of ecological conditions suggest that they are likely to persist. Given the round gobys potential for negative impacts on ecosystem function (as a result of competition with and predation on native species) as well as possible positive impacts on native fish and bird populations (as a result of the availability of a new plentiful food source), it is imperative that efforts to monitor round goby population dynamics, and the factors influencing these dynamics, are maintained. Such efforts will lead to a better understanding of the underlying causes of the trends described here and will shed light on how to control the spread of this invasive species in other water bodies.

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Modelling the Impacts of Male Alternative Reproductive Tactics on Population Dynamics

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Abstract

Much literature has been devoted to understanding the evolution of alternative male reproductive tactics, and to modelling this phenomenon. Most models, however, do not address the consequences of multiple male phenotypes on population dynamics. Here we derive a system of ordinary differential equations to model these impacts on the population dynamics of the invasive round goby (*Neogobius melanostomus*). In this species, some males provide paternal care while other males reproduce by sneaking. We assume that the reproductive success of either male phenotype is influenced by the presence and density of the other. We compare two models: one that assumes that the tactics of offspring are independent of their parent's, and the second assumes that tactics are inherited. We found in both cases that the presence of sneaker males can result in significantly increased populations. We also found that when tactics are not inherited the model always predicts an equilibrium population and, depending on parameter values, can exhibit a threshold density that the population must exceed in order to persist (an Allee effect). When tactics are inherited, the model typically predicts that the population will approach equilibrium either directly, or by damped oscillations. We also found biologically reasonable situations in which it is possible for the population to fluctuate in a continuous, stable cycle. Our results suggest that it is important to incorporate alternative reproductive tactics into population models, particularly for species of environmental or commercial concern.

1 Introduction

Alternative reproductive tactics (ARTs) are a taxonomically widespread biological phenomenon characterized by the existence of two or more discrete reproductive strategies within a population. The existence of two phenotypically distinct male reproductive types (with behavioural, morphological and physiological differences) were first observed in bluegill sunfish, *Lepomis macrochirus* (Dominey, 1980) and field crickets, *Gryllus integer* (Cade, 1979). The coexistence of two or more competing reproductive tactics in a single population challenged the assumption that there is one "best" reproductive strategy, and changed the view of how reproduction evolves (Gross, 1984). Often males will use large size, showy colours or other costly displays to compete for or court females. However, in some species other males exist who lack these morphological, physiological or behavioural traits, and who will instead exploit these courtship investments to achieve reproductive success by use of sneaky or coercive interloper tactics (Oliveira et al., 2008). ARTs have been well-studied as they provide an excellent opportunity to understand evolution and mechanisms underlying phenotypic plasticity; they are examples of discontinuous behavioural and morphological variation in reproduction, and shed light on evolutionary and ecological processes in general (Charnov, 1982; Gross, 1996; Oliveira et al., 2008).

Past modelling efforts have focused predominantly on understanding why and how selection might favour the evolution of ARTs, and how these alternative phenotypes are maintained within a population (reviewed in (Gross, 1996; Oliveira et al., 2008). Game theory has been extensively employed to explore long-term conditions for evolutionary stability and to understand the evolutionary trade-offs between alternative tactics (Gross, 1984; Myers, 1986; Gross, 1996; Repka and Gross, 1995; Lucas and Howard, 2008). Despite the long history of study and the inherent interest in ARTs from an evolutionary perspective, the more immediate consequences of ARTs for population dynamics have rarely been considered (but see Myers, 1984 for an exception).

In this study, we model the effects of ARTs on population dynamics, focusing our attention on an invasive fish species in the Great Lakes, the round goby (*Neogobius melanostomus*). Understanding the short-term impacts of ARTs on the population biology of an agriculturally or commercially important species or a species of conservation concern is essential, and can help us to predict conditions under which we might expect a dramatic increase or extinction. If, for example, male fish employing different tactics are distinguishable by radically different body sizes, then selectively harvesting one male type (either accidentally or intentionally) could have unexpected, undesirable, or even irreversible affects on the population. Myers (1983) showed how fishing pressure could favour the alternative sneaker tactic in Atlantic salmon, potentially having negative impacts on the fishing industry.

Here, we develop an ordinary differential equation (ODE) model to describe population dynamics of a species in which there are two competing reproductive tactics. In particular, we address how the presence of more than one reproductive male tactic influences the expected population size, as well as what changes occur when we vary the model parameter values. We also assess the sensitivity of the model to each of its parameters in order to rank their importance in driving population dynamics. Although our model can be broadly applied to species that express similar ARTs, the parameterization and structure of the model were motivated by the round goby and we will make reference to this species throughout the paper.

2 The round goby

Round gobies were accidentally released from ship ballast water into Lake St. Clair, which is attached to Lake Erie (one of the Great Lakes), around 1990 (Jude et al., 1992). Since then, round gobies have rapidly expanded in both range and abundance to all five of the Great Lakes (Charlebois et al., 2001; Dillon and Stepien, 2001). The successful invasion of the round goby in the Great Lakes constitutes a triple threat because 1) they can out-compete native fish species for food, shelter and breeding habitat (Balshine et al., 2005), 2) they eat eggs and young of other species (Steinhart et al., 2004; French and Jude, 2001) and 3) by virtue of their capacity to eat bivalves they appear to be contributing to toxicant transfer in areas of contamination (Kannan et al., 2005). Round gobies are thought to have contributed to the decline of many native species and to the deterioration of ecosystem health in general (Crossman et al., 1992; Janssen and Jude, 2001). A great deal of time, effort, and money has been spent on preventing round gobies from expanding their range.

Recent research has shown that round gobies exhibit male alternative reproductive tactics (Marentette et al., 2009). Smaller males (sneakers) exploit the effort of larger, nest guarding males (parentals) by sneaking the nests and fertilizing the eggs within, thus avoiding the energy expenditures of both building and guarding the nest (Marentette et al., 2009; Corkum et al., 1998). These ARTs have been recorded and well studied in other species of gobies, including the common goby, *Pomatoschistus microps*, (Magnhagen, 1992), black goby, *Gobius niger* (Mazzoldi and Rasotto, 2002), and the sand goby, *Pomatoschistus minutus* (Svensson, 2004). However, the impacts of ARTs on goby population dynamics have not previously been investigated.

3 ART Background: How are tactics determined?

Phenotypic variation in tactics is thought to originate either from 1) two or more polymorphic genotypes for two strategies co-existing in the population due to balancing selection, or 2) a single genotype existing with two or more emerging phenotypes that are dependent on environmental, developmental or social conditions (Oliveira et al., 2008; Shuster and Wade, 2003). The polymorphic genotype hypothesis proposes that alternative tactics are governed by frequency dependent selection, and have equal mean lifetime fitness (Gross, 1996; Oliveira et al., 2008). If genotype is monomorphic, however, then alternative tactics are governed by conditional (or status) dependent selection, and are likely to have unequal average lifetime fitness (Gross, 1996; Oliveira et al., 2008). In general, conditional strategies are thought to be more common (Gross, 1996).

According to the conditional hypothesis, the reproductive tactic that an individual employs depends on how their condition (or status) with respect to a particular trait relates to a threshold for the population (Gross, 1996). The "decision" of how to allocate reproductive effort can be cued by either environmental, social or developmental conditions (Oliveira et al., 2008). Often, rate of growth or body size at a critical age or time is considered the cue (Garant et al., 2003). The response to this cue could be to either promote or delay sexual maturity (thus adopting one tactic or another), and this is dependent on whether the individual has reached the population threshold size or not (Oliveira et al., 2008). It is assumed that the chosen tactic will provide the highest fitness possible given the size of the individual at some critical time point (Garant et al., 2003; Oliveira et al., 2008; Gross, 1996). Gross (1996) reviewed examples of systems in which tactic choice is determined by reaching such a threshold, but is also influenced by density. Indeed there are theoretical conditions under which ARTs can be evolutionarily regulated by both density and individual status (Repka and Gross, 1995). Our models are formulated such that the fitness of an individual adopting one of two alternative tactics is related to the density of the population.

Also under debate is the extent to which tactics are inherited (i.e., whether offspring express the same phenotype as their parent; Oliveira et al., 2008). If the threshold is related to size, then the reproductive tactic of an individual could be influenced, for instance, by inherited genes affecting growth, or by environmental factors such as feeding conditions. Although we do not directly model individual condition relative to a population threshold, our model could represent a system with a conditional strategy. We will analyze and compare two models; the first assumes that tactics are not inherited, the second assumes that tactics are indeed inherited.

4 Model 1: Tactics not inherited

We begin with the situation where the probability of any given male entering the breeding population as a sneaker or as a parental male is constant and independent of the reproductive strategy of the parent (not inherited). For example, 60% of the males in a clutch of eggs will become parental males and 40% will become sneakers. If tactics are determined by a conditional threshold, then the fixed proportion reflects the fraction of individuals that are above or below the threshold.

Using model 1 (tactics not inherited), we will explore how different proportions of sneaker males will affect population size. For instance, suppose that this fixed probability is related to or regulated by an environmental variable such as food availability. If a change occurs, such as increase in food available, there might also be a change in the ratio of reproductive tactics, and the model can give us insight as to what changes we might expect in the dynamics of the population. This could be of particular interest in fish species like the round goby that has a wide environmental tolerance, and have rapidly expanded their range into many habitats that vary ecologically.

4.1 Environmental and behaviour assumptions

Assumptions made in this model will be based on the behaviour of the round goby, as introduced above. Specifically, we will assume that a male will act either as a parental male (court females, defend their nest and eggs), or as a parasitic sneaker male. We call the fixed probability of becoming a sneaker male α. Both types of males produce sneaker males in the proportion α and parental males in the proportion $(1-\alpha)$. Thus, each new generation will be composed of sneakers and parentals in this proportion. If we make the simplification that both types of males die at the same rate, then α will also become the proportion of sneakers in the total population (which we will call F). The number of sneakers in the population will therefore be $S = \alpha F$, the number of parental males will be $P = (1-\alpha)F$, and the total population, $F = S + P$. Since both P and S can be written in terms of F, our dynamical system can be represented in one dimension, which shows the change in total population size (dF/dt).

Intrinsic reproduction and mortality rates. We suppose that parental males produce young that survive to maturity at intrinsic rate ν_{p},that sneaker males produce young at intrinsic rate ν_{s}, and that both male types die at rate μ. See Table 1 for a summary of parameter definitions. If we were to include only these reproductive and mortality rates in the model then our population would either grow exponentially and indefinitely, or go extinct. If we introduce limited resources, however, competition should lead to density-dependent reproduction.

Limited breeding space. We suppose there is a threshold parental breeding space capacity K_{p}, such that if parental density P is increased towards K_{p} then the reproductive rate of parentals is decreased (reaching zero for $P = K_{\mathrm{p}}$). If P exceeds K_{p} then crowding actually causes the net parental mortality rate to be larger than the intrinsic mortality rate μ. This is formalized with the logistic growth factor,

$$(1 - P/K_{\mathrm{p}})\,. \tag{1}$$

Sperm competition. We expect the presence of sneakers to further hinder parental reproduction through sperm competition (Parker, 1970), and so we show this with the functional response

$$\exp\Big(-S/(L_{\mathrm{p}}P)\Big)\,. \tag{2}$$

This function equals 1 when the sneaker population is zero (no effect of sneakers on parentals) and will approach zero as the sneaker population becomes very large (a very large number of sneakers would severely inhibit reproduction by parentals). In expression (2), L_{p} is a measure of the "resistance" of parentals to the sperm competition experienced from one sneaking attempt. Put another way, it is how strongly the competition from one sneaker reduces successful reproduction for parentals (i.e., the paternity loss from sneaker invasion). If the number of sneakers per parental in the population is L_{p} ($S/P = L_{\mathrm{p}}$), then the presence of sneakers reduces parental reproductive output by a factor of $1/e$. Very small L_{p} implies that the reproductive output of parentals is very strongly hindered by even one sneaker male. Increasing L_{p} (a high resistance) decreases the cost to parental reproduction inflicted by sneakers. Including both factors (competition for space, and from sneakers), the effective rate of reproduction from parental males is represented by

$$\nu_{\mathrm{p}} P \left(1 - \frac{P}{K_{\mathrm{p}}}\right) \exp\left(-\frac{S}{L_{\mathrm{p}} P}\right). \tag{3}$$

Sneaker limit. We also expect that sneakers will compete over available nests to invade. We modify the logistic growth function with a sneaker limit that is proportional to the number of parental males present (and thus to the number of available nests). The reduction in sneaker output from sneaker-sneaker competition thus becomes

$$\Big(1 - S/(L_{\mathrm{s}} P)\Big). \tag{4}$$

While parental males experience competition from sneakers only sometimes, all sneakers experience sperm competition from the parentals that they are sneaking. Thus, the reduction in sneaker output through competition with *parentals* can be included in the sneaker reproductive rate ν_{s}, and an additional density dependent term is not required.

Limited sneaking. Finally, we assume that sneaker male reproduction depends on the presence of parental males, and that it increases proportionally to the availability of nests to invade. We also assume, however, that the number of nests a sneaker can visit is limited (by time, energy, etc.) to at most m_{s} nests per unit time (year). The number of nests a sneaker can sneak must increase from zero (if there are no parentals) to m_{s} (when the number

Table 1: Parameters of the simple model in which tactics are not inherited

Parameter	**Symbol**	**Definition**
parental intrinsic reproductive rate	ν_{p}	rate at which individuals produce offspring that survive to maturity (per year, without resource limitations or competition)
sneaker intrinsic reproductive rate	ν_{s}	
mortality rate	μ	per year (same rate for both male types)
parental breeding space capacity	K_{p}	maximum number of parentals for which there is nest space
parental resistance to paternity loss from sneakers	L_{p}	the degree of reduction in parental reproduction from sperm competition as a result of one sneaker
sneaker limit per parental	L_{s}	maximum number of sneakers per parental (i.e., per nest)
maximum sneaker nest visits	m_{s}	maximum number of nests a sneaker can visit per year

of parentals becomes very large). We incorporate these features by including the factor:

$$f(P) = \frac{m_{\mathrm{s}} P}{m_{\mathrm{s}} - 1 + P} \tag{5}$$

Reproductive output of sneakers thus becomes

$$\nu_{\mathrm{s}} S \cdot f(P) \cdot \left(1 - \frac{S}{L_{\mathrm{s}} P}\right) \tag{6}$$

The model equation. When we combine the reproduction of both sneaker and parental males, and add terms representing natural (density-independent) mortality, we have:

$$\frac{dF}{dt} = \nu_{\mathrm{p}} P \left(1 - \frac{P}{K_{\mathrm{p}}}\right) \exp\left(-\frac{S}{L_{\mathrm{p}} P}\right) + \nu_{\mathrm{s}} S \cdot f(P) \cdot \left(1 - \frac{S}{L_{\mathrm{s}} P}\right) - \mu(P+S)\,. \tag{7}$$

Expressing this directly in terms of the total fish population F, we have

$$\frac{dF}{dt} = F\left[\nu_\mathrm{p}(1-\alpha)\left(1-\frac{(1-\alpha)F}{K_\mathrm{p}}\right)\exp\left(-\frac{\alpha}{L_\mathrm{p}(1-\alpha)}\right)\right. \\ \left. +\nu_\mathrm{s}\alpha\cdot f((1-\alpha)F)\cdot\left(1-\frac{\alpha}{L_\mathrm{s}(1-\alpha)}\right)-\mu\right] \tag{8}$$

Notice that S/P reduces to the constant $\alpha/(1-\alpha)$. This simplifies the equation considerably, and allows us to obtain an explicit formula for all equilibria.

4.2 Analysis of model 1

If model (8) is appropriate for a given biological system, how would we expect the population size to change with time? We show in this section that the model always predicts at least one stable equilibrium toward which we would expect the population to tend.

4.2.1 Existence and stability of equilibria

We first check that the model is well posed (i.e., that it doesn't make biologically absurd predictions, such as negative populations). Since F is a factor of expression (8), the rate of change when $F=0$ will never be negative, so positive initial conditions will never result in negative solutions.

To check for equilibria of this system we set $dF/dt=0$ and solve for F, which yields three equilibria: $F=0$ or $F=F_\pm$, where

$$F_\pm = \frac{1}{2(1-\alpha)^2}\left[-K_\mathrm{p}B \pm \sqrt{(K_\mathrm{p}B)^2 - 4K_\mathrm{p}(1-\alpha)^2(m_\mathrm{s}-1)(ME-1)}\right]. \tag{9a}$$

Here,

$$M = \frac{\mu}{\nu_\mathrm{p}(1-\alpha)}, \tag{9b}$$

$$E = \exp\left(\frac{\alpha}{L_\mathrm{p}(1-\alpha)}\right), \tag{9c}$$

and

$$B = (1-\alpha)\left(\frac{m_\mathrm{s}-1}{K_\mathrm{p}} - 1\right) + \left[\frac{\mu}{\nu_\mathrm{p}} - \frac{\nu_\mathrm{s} m_\mathrm{s} \alpha}{\nu_\mathrm{p}}\left(1 - \frac{\alpha}{L_\mathrm{s}(1-\alpha)}\right)\right] E\,. \tag{9d}$$

$F = 0$ will be an equilibrium point regardless of parameter values, but the remaining equilibria will not always be positive (and hence not always relevant). The stability of all three equilibria will also depend on parameter values (see Appendices A and B for stability conditions and associated proofs). Since we are considering a one-dimensional system, global stability is completely determined by local stability of the equilibria, which is summarized below.

Case 1. (certain extinction): $F_\pm < 0$ or both values are complex. In both instances, we have that $F = 0$ is stable and all populations will go extinct.

Case 2. (certain persistence): $F_- \leq 0 < F_+$. In this case, $F = 0$ will be unstable, and F_+ stable. All positive populations will tend to F_+.

Case 3. (bi-stability, Allee effect): $0 < F_- < F_+$. Here, both $F = 0$ and F_+ will be stable, while F_- will be unstable. The equilibrium population will be determined by how the initial population size relates to F_-; if parameters are such that the initial population is smaller than F_- the population will go extinct, and if it is larger it will tend to F_+. Conditions such as this (where the population must be above some critical threshold to persist) are known as an Allee effect (Courchamp et al., 1999). Here, F_- is the critical threshold below which the population will go extinct.

Note the existence of the marginal case, where $F_+ = F_-$ and $F_\pm > 0$. Here, $F_\pm$ is semistable: all populations larger than $F_\pm$ will tend to this point, and all others will go extinct.

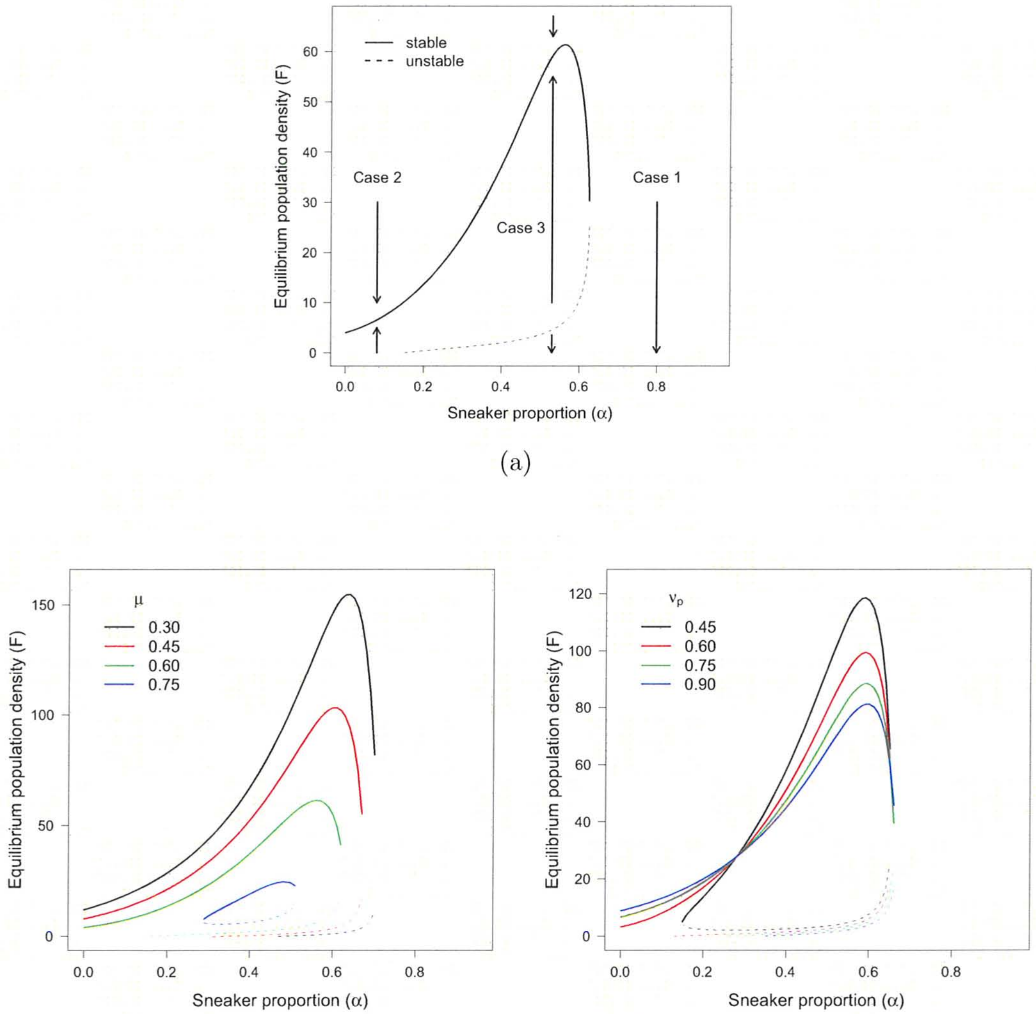
In general, parameter values will determine which of the three cases is realized. If $\mu \geq \nu_\mathrm{p}$ then extinction ($F = 0$) will be stable (but not necessarily globally stable) for all values of $\alpha \in [0,1]$ and we will have case 1 or case 3. Otherwise, $F = 0$ will be unstable for values of α below a certain point, giving case 2 (see Appendix A for details).

4.2.2 Bifurcation diagrams (parameter variation)

Figure 1 is a bifurcation diagram showing all equilibria that exist as a function of sneaker proportion α for a fixed set of the other parameters. Stable and unstable equilibria are specified by solid and dotted curves, respectively. Different colours (in figures 1b and 1c) correspond to different values of one of the fixed parameters. Note that, formally, these equilibria can take negative values, but these are not shown since we are interested only in equilibria that can represent biological populations. Figure 1a shows how regions in the diagram correspond to the three cases of possible dynamics discussed above (1. extinction, 2. persistence, or 3. Allee effect).

Regardless of which parameter is varied, the basic shape of the bifurcation diagrams (as in Figure 1) remains relatively similar throughout. Specifically, the presence of sneakers (i.e., when $\alpha > 0$) tends to result in a larger equilibrium population than when the proportion of sneaker males is zero. Increasing the proportion of sneakers (α) continues to increase the population until a threshold proportion after which the population cannot be sustained. Above this value there are no positive equilibria, and all initial conditions result in extinction. We will call this α the crash threshold. The α at which the population reaches its maximum possible value we will call α^*. It can be described analytically as the point at which the derivative of F_+ (with respect to α) is zero. Finally, we are also interested what happens if we impose $\alpha = 0$ (i.e., there are no sneaker males). Here, if $\mu < \nu_\text{p}$ (i.e.. mortality rate is lower than the intrinsic rate at which parentals reproduce) we find a sneaker free equilibrium. This equilibrium happens at $F = K_\text{p}(1 - \mu/\nu_\text{p})$.

Through bifurcation diagrams such as in Figure 1 we find that the model can predict some unexpected dynamics. First, we find that sneakers can cause the population to persist when it would go extinct in their absence. Consider the curve in Figure 1b associated with $\mu = 0.75$ (which is also the value for ν_p in this figure). As we would expect, since the parental reproductive rate is not higher than the mortality rate, parentals are not replacing themselves and there is no positive equilibrium at $\alpha = 0$ (i.e., no sneaker free equilibrium). However, if there is a certain proportion of sneaker males in the population (α approximately between 0.3 and 0.5, in this case), then the reproduction from sneaker males is sufficient to compensate for the low reproduction of parental males, and the population can persist. This may seem peculiar, but recall that sneaker males also produce parental males. This result is of interest when considering conservation strategy; artificially increasing the



(a)

(b)

(c)

Figure 1: Example bifurcation diagrams for the tactics not inherited model (8): Equilibrium population size, $F_{\pm}$ (9a), as a function of fixed sneaker proportion α. Solid lines represent stable equilibria (F_+), dashed lines are unstable (F_-). (a) Arrows show the direction in which populations will tend. Cases correspond, respectively, to extinction, persistence, and bi-stability (two stable solutions). The last case is an example of an Allee effect; populations above a threshold density will persist, but will otherwise go extinct. (b) Colours correspond to different values of mortality rate, μ, or (c) parental intrinsic reproductive rate, ν_{p}. All other parameters (Table 1) are held constant: $\nu_{\text{s}} = \nu_{\text{p}} = .75$, $\mu = .5$, $K_{\text{p}} = 20$, $L_{\text{p}} = L_{\text{s}} = m_{\text{s}} = 3$.

mortality rate will not be as effective if the proportion of sneakers is such that the population can persist.

We also find, counterintuitively, that for higher α values, increasing the reproductive output of parental males can actually cause a decline in the population (Figure 1c). This happens when we increase parental reproduction either by increasing the parental intrinsic reproductive rate (ν_{p}), or by increasing parental resistance to sperm competition from sneaker males (L_{p}). To see why this happens, consider the parental reproduction term in expression (8). This term will be negative whenever $F > K_{\text{p}}/(1-\alpha)$ (i.e., whenever the number of parental males have exceeded the parental breeding space capacity). So, suppose that the population has reached equilibrium F_+, and that this equilibrium is greater than $K_{\text{p}}/(1-\alpha)$ (in Figure 1c, this is true for proportions roughly between 0.3 and 0.6). Increasing ν_{p} or L_{p}, in this case, will make the parental reproduction term more negative, resulting in a smaller population size. More simply put, if there is insufficient space for parentals to breed, then an increase in their reproductive success will cause the population to settle at a smaller density to compensate.

4.3 Global parameter sensitivity: Importance of parameters

Bifurcation diagrams such as those in Figure 1 can be interpreted as local sensitivity analysis; one parameter is varied while holding the rest constant. To get a sense of which parameters are most important in the model (i.e., when varied, which parameters result in the largest changes in population size), we use global sensitivity analysis (SA). This technique allow us to vary all parameters simultaneously and, similar to an ANOVA, estimates how much of the variance in population size can be attributed to each parameter (or factor). See Appendix D for details of this statistical method.

Here we use two statistical techniques to assess the model outputs (stable equilibria), which are calculated using parameters chosen from the ranges listed in Table 2 (See Appendix C for a discussion of the chosen parameter ranges). Standardized regression coefficients (SRCs) were used to determine the direction of influence for each parameter (i.e., if we increase the parameter value, would we expect an increase or decrease in the equilibrium population; Saltelli et al., 1999; Ellner and Guckenheimer, 2006). To quantify the relative magnitude of influence that each parameter has on the model output, we use

Table 2: Model parameter ranges for Sensitivity Analysis

Parameter	α	$\nu_{\mathrm{p}}, \nu_{\mathrm{s}}, \mu$	K_{p}	$L_{\mathrm{p}}, L_{\mathrm{s}}$	m_{s}
Range	$[0 - 0.95]$	$[0.33 - 1]$	$[20 - 25]$	$[1 - 10]$	$[1.1 - 10]$

a variance decomposition technique called FAST (Saltelli et al., 1999), which is similar to an ANOVA and estimates how much of the output variance (the dependent variable) can be attributed to each parameter (or factor). From this we can glean the following (Saltelli et al., 2004):

- **The main effect index (M_i):** by what proportion would the variance in the output be reduced if the parameter in question were known (and fixed). This is used for *factors prioritization*
- **The total effect index (T_i; main effect plus interactions):** what fraction of variance would be *left* if all other factors were fixed. It is used for *factor fixing*; factors with a low total index are non-influential and can be fixed at any value in the assessed range

A detailed global sensitivity analysis revealed that when parameters are chosen from the full ranges in Table 2, no single parameter explains more than 4% of the variance, but all parameters interact strongly with one another (all $M_i < 0.04$, all $T_i > 0.3$ except for $T_{K_{\mathrm{p}}} = 0.04$). If we consider smaller intervals for α (of length 0.1), however, we can better see which parameters are driving the model. The ranked influence of each parameter is summarized in Table 3, which shows the parameters having the most direct influence on population size (largest M_i) as well as the lowest overall influence (smallest T_i)

While α was never one of the most significant parameters, the direction of its influence was always positive; on average, increasing the proportion of sneakers will result in the population tending toward a higher equilibrium. In general, nearly all parameters affect the equilibrium population in a positive direction. There are two notable exceptions (other than mortality rate, μ); increasing parental reproductive rate (ν_{p}) will, on average, suppress the population when sneaker proportion is above 0.1 (as in Figure 1c). The result is the same for parental resistance to sneakers (L_{p}). Note, however, that neither of these exceptional parameters are ranked strongly in importance, but instead are often among the least influential (Table 3). In other words, while increasing either parameter will tend to decrease the equilibrium population,

Table 3: Results of sensitivity analysis (methods described in Appendix D) for the tactics not inherited model. Parameters with high main effect indices (M_i, priority factors), and those with low total effect indices (T_i, fixable factors) are shown. Parameter rankings differ depending on the sneaker proportion and are grouped accordingly. See Table 1 for parameter definitions.

	Sneaker proportion (α) ranges			
Sensitivity index range	$(0-0.1)$	$(0.1-0.2)$	$(0.2-0.4)$	$(0.4-0.6)$
$M_i \geq 20\%$	μ	μ	ν_{s}, m_{s}	m_{s}
$10\% < M_i < 20\%$	ν_{p}	ν_{s}, m_{s}	(μ)	ν_{s}
$T_i \leq 5\%$	K_{p}, ν_{s} L_{s}, L_{p}	K_{p} L_{s}, L_{p}	K_{p} (L_{s}), L_{p}	K_{p}, μ

the magnitude of this decrease will be small compared to changes resulting from those parameters mentioned in the table.

Note that Table 3 does not show α values above 0.6. This is because any individual parameter influence for these ranges is masked by strong interactions. No parameters affect more than 10% of the variance directly (all $M_i < 0.1$), and no paramters could be fixed (all $T_i > 0.06$). Also note that parental breeding space capacity (K_{p}) was chosen from a narrow range to avoid masking the influence of other parameters. If a larger range for K_{p} is assessed, then this parameter has a much larger influence on population size.

The maximum sustainable proportion of of sneakers (the crash threshold) as well as the proportion at which the population size can be maximized (α^*), were both most strongly influenced by the maximum number of sneakers per parental (L_{s}; $M_{L_{\mathrm{s}}} = 0.30$ and 0.35 for crash threshold and α^* respectively, all other $M_i < 0.09$). This result is logical since if $\alpha > L_{\mathrm{s}}/(1 + L_{\mathrm{s}})$, sneaker reproduction will always be negative (because at these proportions sneakers are always exceeding their limit as it has been defined). Increasing L_{s} therefore represents an increase in the proportion of sneakers that the population can sustain, as well as an increase in the proportion of sneakers that will maximize the population.

4.4 Summary

Assuming that reproductive tactics are not inherited leads to a one-dimensional model (8) which predicts three possible equilibrium populations. 1) the population will go extinct, 2) the population will certainly persist, or

3) there is a threshold above which the population will persist, and below which it will go extinct (Allee effect). Although we are unlikely to observe a true equilibrium population in nature, if model (8) is appropriate for a given biological system, we can expect the population to tend toward the equilibria predicted by the model. Furthermore, observations about how the equilibrium population is affected by a change in parameter value can offer insight into how we might expect the population to react to real perturbations in the system, such as an increase in predation or food, or in the fixed proportion of sneakers.

This model predicts that increasing the proportion of sneaker males (α) will tend to result in a substantially larger equilibrium population (as in Figure 1). There is however, a threshold proportion of sneakers above which the population cannot be sustained. This proportion depends on parameter values and the maximum number of sneakers per parental (L_s) in particular.

The proportion of sneakers also influences which parameters in the model are most important. If the sneaker proportion is low changes in mortality rate (μ) will have the largest impact on the population size. If α is between 0.2 and 0.6, we expect changes in sneaker intrinsic reproductive rate (ν_s) or maximum sneaker visits (m_s) to be the most influential. Given that we have chosen parameter ranges that reflect the population in question, these results could be used to prioritize the allocation of resources for parameter estimation, and also, in the case of our focal species, to inform decisions about invasive management strategy.

5 Model 2: Tactics inherited

In the previous section, we made the simple assumption that the phenotype of the offspring is completely independent of the phenotype of the parent. In this section we consider the consequences on population dynamics when reproductive tactics are inherited. We make a simplifying assumption that phenotypes of offspring are *completely* determined by that of the male parent (i.e., sneakers will produce only sneaker males, and parentals will produce only parental males). As with the tactics not inherited model, we can suppose that tactic choice is being determined by whether the condition of an individual is above or below some threshold. In this scenario, however, the relevant trait is inherited, so that individuals that were above the threshold will produce offspring that are also above the threshold, and individuals below the threshold will produce offspring that are likewise below.

The first consequence of this formulation, which allows the proportion of sneakers to be dynamic rather than fixed, is that we require two equations (one for each male type) to describe the population size. We retain all assumptions from section 4.1 except for that of tactic inheritance. Additionally, we allow the mortality rate of the two male types to differ. Our new model is thus:

$$\frac{dP}{dt} = \nu_{\mathrm{p}} P \left(1 - \frac{P}{K_{\mathrm{p}}}\right) \exp\left(-\frac{S}{L_{\mathrm{p}}P + 1}\right) - \mu_{\mathrm{p}} P \tag{10a}$$

$$\frac{dS}{dt} = \nu_{\mathrm{s}} S \frac{m_{\mathrm{s}} P}{m_{\mathrm{s}} - 1 + P} \left(1 - \frac{S}{L_{\mathrm{s}}P + 1}\right) - \mu_{\mathrm{s}} S \tag{10b}$$

Compared with the simpler model (8), note that L_{p} has been replaced by $L_{\mathrm{p}} + 1$ here to avoid dividing by zero if $P = 0$. The total fish population size is $F = P + S$.

5.1 Model analysis: Equilibria and example dynamics

5.1.1 Analytical Equilibria

We first note that this model is well posed; if $P = 0$ then $dP/dt = 0$ also. Similarly, if $S = 0$, $dS/dt = 0$, and so non-negative initial conditions will never result in negative solutions.

Since we have two equations (a two-dimensional system), any equilibria will be represented by a point (P_*, S_*) in the (P, S) phase plane, where P_* is the equilibrium parental density and S_* is the equilibrium sneaker density. The total population at equilibrium is $F_* = P_* + S_*$. We find equilibria by setting $dP/dt = 0$ and $dS/dt = 0$ simultaneously and solving the system for P and S.

In this way we find two equilibria analytically, the first of which represents extinction; $(P, S) = (0, 0)$. We determine the stability of an equilibrium point by evaluating the Jacobian matrix of the system (10) at the point in question, calculating its eigenvalues, and observing their signs. Doing so for the extinction equilibrium gives eigenvalues $[\nu_{\mathrm{p}} - \mu_{\mathrm{p}}, \ -\mu_{\mathrm{s}}]$, and so $(0, 0)$ is a stable sink (i.e. both eigenvalues are negative) when $\mu_{\mathrm{p}} > \nu_{\mathrm{p}}$, and an unstable saddle when $\mu_{\mathrm{p}} < \nu_{\mathrm{p}}$. That is, if the parental mortality rate is greater than the parental intrinsic reproductive rate, then all nearby solutions will crash to zero (i.e. the population will go extinct). If parental mortality is less than their reproductive rate, then all nearby solutions will tend away from $(0, 0)$ except when $P = 0$; when the parental population is zero, then the sneaker population must tend to zero as well.

More generally, if $S = 0$ we find an analytical solution for P, giving a sneaker-free equilibrium very similar to that of the tactics not inherited model: $(P,\ S) = (K_\mathrm{p}(1 - \mu_\mathrm{p}/\nu_\mathrm{p}),\ 0)$. The population will tend to this point when both associated eigenvalues are negative, which happens when the following are satisfied:

$$\frac{m_\mathrm{s} K_\mathrm{p}(\nu_\mathrm{p} - \mu_\mathrm{p})}{\nu_\mathrm{p}(m_\mathrm{s} - 1 + K_\mathrm{p}) - \mu_\mathrm{p} K_\mathrm{p}} < \frac{\mu_\mathrm{s}}{\nu_\mathrm{s}} \quad \text{and} \quad \mu_\mathrm{p} < \nu_\mathrm{p} \tag{11}$$

In other words, the sneaker population will die out, leaving a positive parental population, if the ratio between their intrinsic reproductive and mortality rates is sufficiently low, and if parental intrinsic reproductive rate is greater than parental mortality rate (i.e., when $(0, 0)$ is unstable). Note that this condition is independent of both sneaker limit (L_s) and parental resistance to sneakers (L_p).

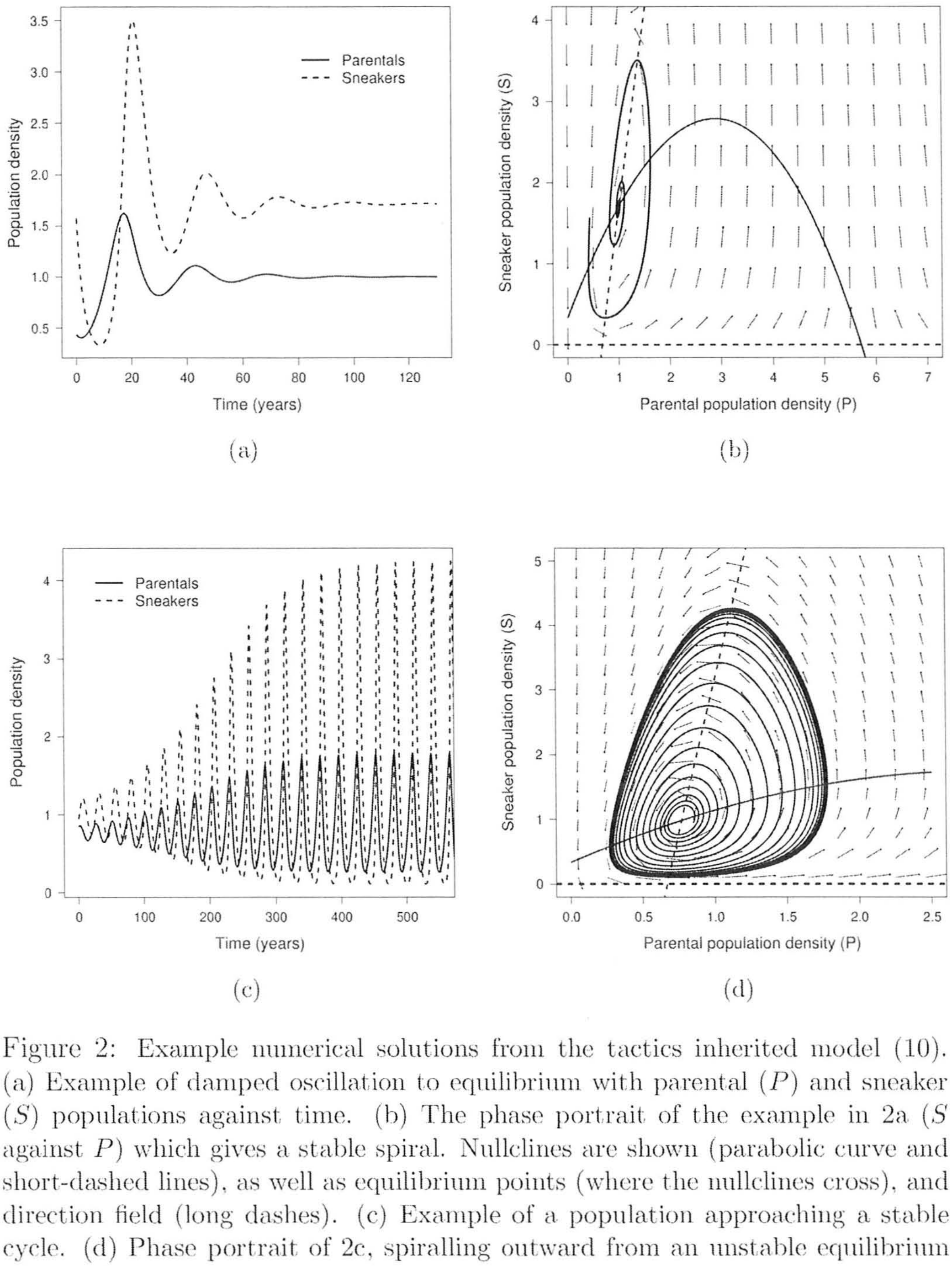
5.1.2 Numerically determined equilibria

Any further equilibria will have both P and S nonzero (coexistence), and must be estimated numerically. We found such points by first solving $dS/dt = 0$ to find the equilibrium value S_* as a function of P, and substituting this formula into $dP/dt = 0$ before solving numerically for the equilibrium value P_*. Stability of these points was determined by assessing the eigenvalues at the numerically determined equilibrium.

We find that there is at most one coexistence equilibrium (both P and S positive), and it will be present when

$$\frac{\mu_\mathrm{s}(m_\mathrm{s} - 1)}{\nu_\mathrm{s} m_\mathrm{s} - \mu_\mathrm{s}} < K_\mathrm{p}\left(1 - \frac{\mu_\mathrm{p}}{\nu_\mathrm{p}}\right). \tag{12}$$

(see Appendix E for proof). Through numerical bifurcation analysis we observed three different dynamics around this coexistence equilibrium (discussed in more detail in the following section). In two of these scenarios the coexistence equilibrium is stable, and is approached either as a spiral or as a source. Figure 2a shows an example (numerical) solution of the former case; it shows the sneaker and parental population against time and illustrates



(a) (b)

(c) (d)

Figure 2: Example numerical solutions from the tactics inherited model (10). (a) Example of damped oscillation to equilibrium with parental (P) and sneaker (S) populations against time. (b) The phase portrait of the example in 2a (S against P) which gives a stable spiral. Nullclines are shown (parabolic curve and short-dashed lines), as well as equilibrium points (where the nullclines cross), and direction field (long dashes). (c) Example of a population approaching a stable cycle. (d) Phase portrait of 2c, spiralling outward from an unstable equilibrium to a stable cycle.

the damped oscillation to the equilibrium point. Figure 2b shows the phase portrait of this example. The sneaker-free and the extinction equilibria are saddle points in this case; all initial condition such that $P = 0$ or $S = 0$ tend toward the extinction or sneaker-free points respectively, and all others tend toward the coexistence equilibrium. The third dynamic observed was an unstable equilibrium point surrounded by a stable cycle. An example solution of this type is shown in Figure 2d, with the population plotted against time in Figure 2c. Note that these examples all show solutions where the mortality rates are equal ($\mu_\text{p} = \mu_\text{s}$) for ease of comparison with the tactics not inherited model.

5.2 Parameter variation

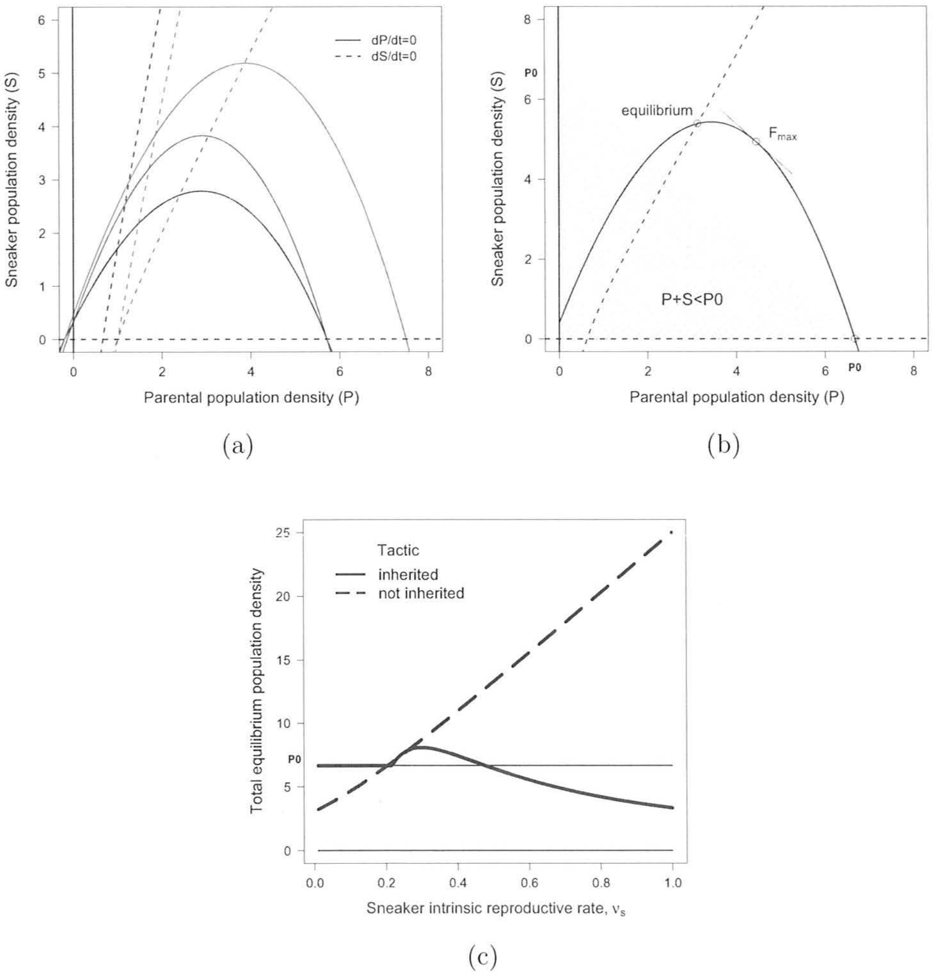
5.2.1 Nullclines and local bifurcations

To better understand the conditions under which the different dynamics occur, as well as how the equilibrium population is affected, we look at how the nullclines change with variation of parameter values. The short-dashed lines and solid down-turned curves in figures 2b and 2d represent the nullclines in these examples; they are the points in the $PS-$plane at which either $dP/dt = 0$ or $dS/dt = 0$, and so the place where they cross shows the equilibrium values for P and S. The equations for the P and S nullclines respectively are below.

$$S(P) = -\ln\left(-\frac{\mu_\text{p} K_\text{p}}{\nu_\text{p}(P - K_\text{p})}\right)(L_\text{p} P + 1) \tag{13a}$$

$$S(P) = PL_\text{s} + 1 - \frac{\mu_\text{s}}{\nu_\text{s}}\left[L_\text{s} + \frac{1}{P} + \frac{1}{m_\text{s}}\left(-L_\text{s} - \frac{1}{P} + L_\text{s} P + 1\right)\right] \tag{13b}$$

Adjusting parameter values and observing how these nullclines (and thus the equilibrium populations) change reveals a great deal about the behaviour of the system. For instance, we see immediately that changing parental related parameters (ν_p, μ_p and L_p) affects the curved (solid) nullcline (13a), while varying sneaker related parameters (ν_s, μ_s, L_s and m_s) affects the straighter (dashed) nullcline (13b). Figure 3a summarizes the movement of the nullclines in relation to parameter changes. Increasing ν_p (or decreasing μ_p) expands the curved nullcline (solid black to red), and increasing L_p inflates the height of the same (solid black to blue). On the other hand in-



(a) (b)

(c)

Figure 3: (a) Example nullclines for the tactics inherited model (10). Dashed curves are nullclines associated with sneaker related parameters (resulting from $dS/dt = 0$, expression (13b)), solid curves (solution for $dP/dt = 0$, 13a) are affected by parental parameters. Increasing $\nu_{\rm p}$ gives solid black to red; increasing $\nu_{\rm s}$, dashed red to black; increasing $L_{\rm p}$, solid black to blue; increasing $L_{\rm s}$, dashed blue to red (see Table 1 for parameter definitions). (b) An example equilibrium and the associated maximum potential equilibrium population ($F_{\max}$). Also shown: sneaker-free equilibrium ($P0$) and region in which the total population is less than the associated sneaker free population ($S + P < P0$) (c) Equilibrium total populations for tactics inherited and tactics not inherited models as a function of sneaker intrinsic reproductive rate ($\nu_{\rm s}$). The horizontal line denoted by $P0$ represents the sneaker free equilibria. Remaining parameters set at: $\alpha = .2$, $\nu_{\rm p} = .75$, $\mu_{\rm p} = \mu_{\rm s} = .5$, $K_{\rm p} = 20$, $L_{\rm p} = 5$, $L_{\rm s} = m_{\rm s} = 3$.

creasing ν_s (or decreasing μ_s) moves the straighter nullcline to the left (dashed red to black), as does increasing L_s (dashed blue to red) or m_s (not shown).

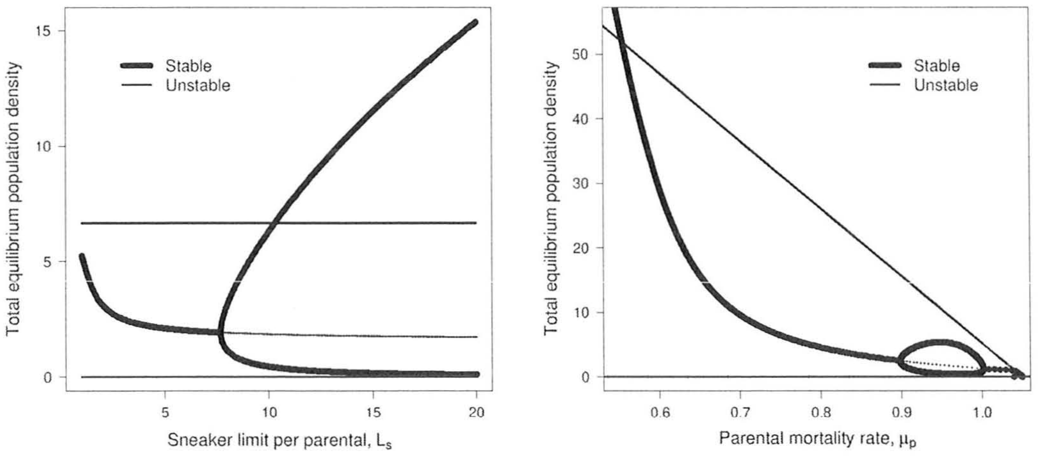
To see how these movements affect the total population at the coexistence equilibrium point, note that the parental population is maximized when the equilibrium is at the point where the parental nullcline crosses the P-axis (denoted by $P0$ in Figure 3b), and the sneaker population is maximized at the peak of the same curve. The total population ($F = S + P$) is maximized between these two points, when the tangent to the curve has a slope of -1 (F_{max} in Figure 3b). To see why, consider a straight line with slope -1. This represents points where $P + S = c$ where c is some constant. For P and S closer to the origin than this line, we have $S + P < c$. If we slide this line of slope -1 from infinity toward the curved nullcline, it must be tangent at the point where it first touches the nullcline. Thus all other coordinates on the nullcline will have smaller sums.

Increasing the success of parentals (stretching the parental nullcline) tends to result in an increased total population. Increasing sneaker success, however, moves the sneaker nullcline (dashed line) to the left, which often moves the equilibrium away from F_{max}. In other words, increasing the success of sneakers often results in a suppression of the total population. The shaded region of the diagram shows all possible equilibrium populations for which the sum of parental and sneakers males would be less than the sneaker-free equilibrium. That is, if parameters are such that the equilibrium value is found inside this region, then the presence of sneakers has resulted in a smaller population size than would a population of only parental males.

The effects of improving sneaker success differ dramatically depending on whether reproductive tactic is inherited. Figure 3c compares the effects of increasing sneaker intrinsic reproductive rate (ν_s) between the two models. The parameter values are identical for both bifurcation diagrams, with sneaker proportion fixed at $\alpha = 0.2$ for the tactics not inherited model. Note that the tactics inherited model predicts a population below the sneaker free equilibrium (horizontal thin line at $P0$) much more frequently than does the tactics not inherited model.

5.2.2 Conditions for a stable cycle

The coexistence equilibrium point is not always stable but instead occasionally becomes an unstable point oscillating toward a stable cycle (i.e., a supercritical Hopf bifurcation occurs). To determine when such dynam-



(a) (b)

Figure 4: Bifurcation diagrams for the tactics inherited model (10) plotting total equilibrium population (parental plus sneaker) against (a) maximum number of sneakers per parental (L_s) and (b) parental mortality (μ_p). Wherever there are two stable (thick) lines at the same parameter value, they represent the maximum and minimum populations in a stable cycle. Unstable lines in between these are the unstable equilibrium at the centre of the spiral, as in figure 2d. The sneaker free equilibrium is (a) the horizontal line at $y = 8$ or (b) the narrow line with negative slope. These diagrams were made using XPPAUT version 5.9 (Ermentrout, 2002). Remaining parameter values were set at: (a) $\nu_p = \nu_s = .75$, $\mu_p = \mu_s = .5$, $K_p = 20$, $L_p = m_s = 3$. (b) $\nu_p = 1.05$, $\nu_s = 0.52$, $\mu_s = 0.49$, $K_p = 109.9$, $L_p = 6.23$, $L_s = 4.97$, $m_s = 3.22$.

ics occur, we numerically calculated the equilibria associated with several thousand randomly drawn sets of parameters, assessed their stability, and observed patterns in those sets which produced unstable equilibria (with a stable cycle). We find at least two distinct parameter spaces in which a Hopf bifurcation occurs.

Figure 4a shows a bifurcation from stable point to unstable cycle as L_s is increased (maximum sustainable number of sneakers per parental). It appears to be true in general that the equilibrium is destabilized in this way when L_s is sufficiently larger than L_p (parental resistance to sneakers). This is a biologically plausible situation where parental males are severely affected by the presence of sneakers (because of inferior sperm, for instance), but it takes a larger number of sneakers per nest (higher L_s) before competition with other sneakers severely inhibits their success. We show a second situation in which the increase of parental mortality (μ_p) causes a Hopf bifurcation (Figure 4b). This time, the equilibrium regains stability (reverse supercritical Hopf bifurcation) as μ_p approaches ν_p, and as the total population approaches zero. Recall that when $\mu_\mathrm{p} = \nu_\mathrm{p}$ the extinction equilibrium will become stable. Note in this example that once again, the equilibrium population (thick line) is smaller than the sneaker-free population (thin line). This situation appears, generally, to occur when parental mortality (μ_p) is sufficiently high compared to sneaker reproductive and mortality rates (ν_s and μ_s).

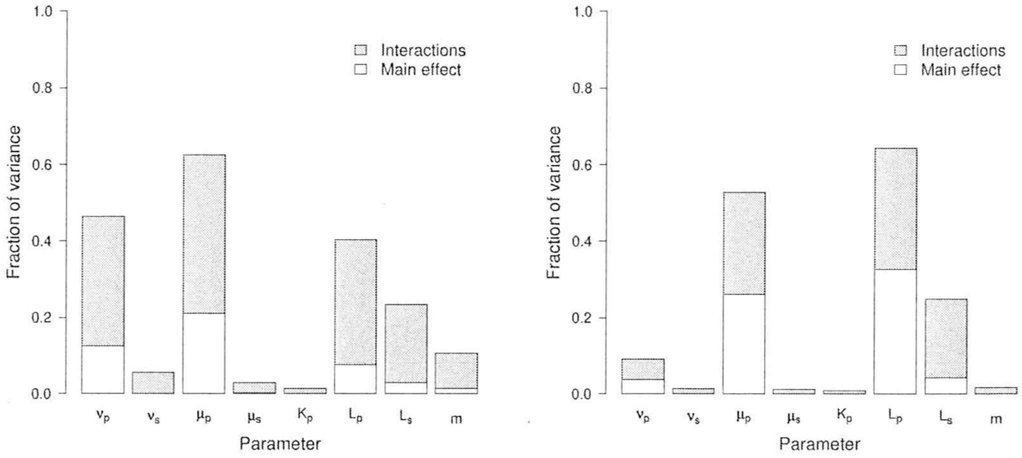
5.2.3 Global parameter sensitivity

We next use global sensitivity analysis to summarize the relative magnitude of change, resulting from variation of each parameter, in the coexistence equilibrium discussed above. Since this equilibrium is not always stable, we are not necessarily assessing changes in final equilibrium population size; the equilibrium population may actually oscillate (in a stable cycle) around the point being assessed. Nevertheless, we can still get an overall picture of which parameters are most influential. We are also interested, in this case, in how parameter changes might influence the proportion of sneakers at the coexistence equilibrium. For global sensitivity analysis (see Appendix D) we take parameters from the same ranges as for the tactics not inherited model (table 2) with two exceptions; we take K_p from $[100-120]$, and we lower the minimum values for L_p and L_s to 0 (which can be done in this case because of the $+\ 1$ that was added to the denominator).

Standardized regression coefficients for the coexistence equilibrium tell us that, on average, increased reproductive success (or survival) of parental males will result in an increased total equilibrium (i.e., increasing ν_{p} or L_{p}, or decreasing μ_{p}). On the other hand, an increase in sneaker reproductive success (increase in ν_{s}, L_{s}, or m_{s}, or a decrease in μ_{s}) will on average tend to lower the total equilibrium (as in Figure 3c). This could pose a problem for conservation strategies if selective harvesting of parental males is not possible or economically feasible; harvesting sneaker males could counter the effects of harvesting parental males. However, an analysis of variance (using FAST) reveals that none of these parameters has a strong influence on the total equilibrium (Figure 5a). In fact, both sneaker reproductive rate and mortality (ν_{s}, μ_{s}) have very low total effect indices, and could therefore be fixed at any value in the assessed range. Instead, we find that parental related parameters have much more influence on this model output. In particular, parental mortality (μ_{p}) strongly influences the equilibrium.

Figure 5b compares results when we choose reproductive rates to be larger than mortality rates (ν_{p}, ν_{s} from $[1.33-2]$). While parental resistance to sneakers (L_{p}) becomes the most important parameter in this range, the influence of parental mortality is not diminished. This is good news for conservation strategy; for either true parameter range, this model predicts that selectively harvesting parental males will result in a reduction in the total population, and the reduction will be appreciable. Furthermore, if sneakers are also harvested, and if this harvest results in an increase in the equilibrium, we would not expect this to counter the decrease in the equilibrium from the harvesting of parental males. On the other hand, as seen in the previous section, harvesting parental males (i.e., increasing the mortality rate μ_{p}) could have the unintended consequence of destabilizing the population (Figure 4b).

We also look briefly at the effects of parameter variation on the equilibrium proportion of sneakers. Unexpectedly, increasing ν_{p} also increases (on average) the the equilibrium sneaker proportion (the SRC is positive); allowing parentals to reproduce more successfully tends to result in a higher sneaker to parental ratio. The parameters that most influence sneaker proportion differ for the two considered parameter ranges. When reproductive and mortality rates are selected from the same range, sneaker proportion is most influenced by the same parameters that determine population size ($M_{\nu_{\mathrm{p}}} + M_{\mu_{\mathrm{p}}} = 0.63$). When reproductive ranges are higher than mortality ranges, however, sneaker proportion is almost completely determined by L_{s},



(a) (b)

Figure 5: (a) Sensitivity indices (from variance decomposition, Appendix D) for the tactic inherited model (10), with parameters as assessed in the ranges listed in Table 2, with exceptions discussed in section 5.2.3. Each bar represents the fraction of variance in the model output (total equilibrium, sneakers plus parentals) attributed to each parameter, with both main effect and interactions (total minus main) shown. (b) Sensitivity indices with both sneaker and parental intrinsic reproductive rates (ν_{p} and ν_{s}) assessed in a range exceeding mortality rates ($[1.33, 2]$).

sneaker limit ($M_{L_s} = 0.82$). Note that this result refers only to the parameter influence on the coexistence equilibrium, whether it is stable or not. However, since this parameter (L_s) is also one parameter that can result in a stable population cycles when sufficiently large, we might conclude that this parameter is indeed strongly influencing the proportion of sneakers in the population.

5.3 Summary

The assumption of inherited tactics leads to a two-dimensional model (10) in which the proportion of sneaker males can change. This model predicts three biologically relevant scenarios: 1) extinction, 2) a population in which there are only parental males, or 3) a population where parental and sneaker males co-exist. In the third case, there are two possible scenarios for the coexistence of two phenotypes. More often, the populations of sneaker and parental males will approach a stable coexistence equilibrium, and will do so via damped oscillations. Occasionally, the coexistence equilibrium will be unstable, resulting in stable population cycles. This last dynamic seems, in general, to occur in two parameter regimes. The first is when the cost of sneaker males to the success of parental males is sufficiently greater than the cost to sneakers of competition with other sneakers (i.e., $L_s > L_p$). The second situation is when the parental mortality rate (μ_p) is sufficiently large compared to the sneaker intrinsic reproductive rate (ν_s).

In general, increasing parental reproductive success or survival results in an increase in the total population at the coexistence equilibrium. Conversely, improving sneaker success or survival more often than not lowers that total and, if it is a stable point, suppresses the total equilibrium population. Sneaker related parameters, however, are largely non-influential on the total at the coexistence equilibrium. Instead, the most important parameters in this model are those related to parental reproduction: reproductive rate (ν_p), mortality rate (μ_p) and parental resistance to sperm competition from sneakers (L_p). In other words, if one were to harvest round gobies, but a differentiation between sneaker and parental males was not possible, the potential increase in population from the harvesting of sneaker males is predicted to be small compared to the decrease from harvesting parentals (resulting in an overall decrease in the population). It is important to note however, that the harvesting of parental males could also act as a destabilizing pressure, as noted above, leading to stable population cycles.

6 Conclusions and Discussion

6.1 Comparing models: Tactic inherited versus not

Many studies investigating alternative reproductive tactics focus on uncovering the causal mechanisms or evolutionary trade-offs associated with different phenotypes, either experimentally or with evolutionary modelling (reviewed in Oliveira et al., 2008). Here, we have accepted that alternative tactic have evolved, and attempted to answer questions about how competition between two phenotypes might affect the population size and population dynamics in general. While we have developed the models based on the competing sneaker and parental male phenotypes of the round goby, they could be more broadly applicable to any system in which some males exhibit parental care while others reproduce by exploiting these costly efforts.

We found that the presence of alternative reproductive tactics can strongly affect the dynamics of a population. Comparing two models in which tactics are either inherited, or not inherited, we found both models predicted that a population containing an alternative tactic (e.g. sneaker males) could potentially have a greater total size than a population with only one type of reproductive male (parental males). The magnitude of this potential increase, however, was much greater under the assumption that reproductive tactics are not inherited (when the probability of being born a sneaker was fixed). In the case where tactics are inherited, the population was more likely to be suppressed by the presence of a second phenotype.

When tactics are assumed to be inherited, the proportion of sneakers can change and we often observe an oscillation of both parental and sneaker phenotypes, as well as in the total population, that was not seen in the tactics not inherited model. Furthermore, this oscillation could become a stable population cycle. The conditions for this last dynamic are either 1) that the loss of reproduction to parentals that have been invaded by sneaks is large compared to the loss of reproduction to a sneaker from competition with other sneakers, 2) that parentals are dying at a rate that is sufficiently large compared to the rate at which sneaker males are reproducing. If tactics were not inherited, we found that given certain sneaker proportions (α), the population could exhibit an Allee effect, where the persistence or extinction of the population depended upon the population size. We did not observe an Allee effect in the tactics inherited model.

Finally, the two models also differ in how the variation of parameters affects their equilibria. When tactics are not inherited, the equilibrium population size is most influenced by parameters relating to sneakers. Namely, sneaker reproductive rate (ν_{s}) and maximum sneaker visits (maximum number of nests a sneaker can visit per unit time, m_{s}) had the strongest effects whenever sneaker proportion was fixed to be higher than 0.2. When tactics are inherited, however, these parameters have little consequence on the coexistence equilibrium, and could therefore be fixed at any value in the assessed range. Instead, the model is very strongly driven by parental intrinsic reproductive and mortality rates (ν_{p}, μ_{p}), as well as parental resistance to sneaker males (the cost of the presence of sneakers to parental reproduction, L_{p}). The ranked importance of parameters is of interest when allocating resources for parameter estimation or considering conservation strategy or commercial fishing policy. Under the assumption of inherited tactics, our model would suggest that efforts to inhibit an invasive species like the round goby might be best focused toward decreasing the survival of parental males. If, instead, we were interested in commercially harvesting a species without reducing the population, then this model would suggest that increasing the mortality of sneaker males would cause the smallest decrease in population size.

As a note of caution, analyses of parameter sensitivities are subject to the parameter ranges chosen, and results can differ a great deal if these ranges are changed. We have assessed reproductive and mortality rates from the same range, and as a result the analysis is likely revealing which parameters most strongly affect whether the population crashes or persists. If we were assessing parameter ranges that always resulted in a zero equilibrium (if, for instance, we were evaluating a species in decline), then we would need to assess a model output other than equilibrium to obtain insightful results. For example, we might evaluate the predicted population after some time t, or the average population.

Experimental estimates of the parameters in this model are required for more meaningful (and applicable) sensitivity assessment. Namely, survival to maturity, which would include estimates of juvenile survival, combined with egg yield and survival of young. In addition, paternity studies on the degree of sperm competition between parental and sneaker males could also contribute to better estimates of sneaker intrinsic reproductive rate (ν_{s}) and to understanding the cost of the presence of sneakers to parentals (L_{p}). The level of sperm competition experienced between sneaker males would also inform estimates of the maximum number of sneaker males per parental that can be sustained (L_s).

6.2 Future work

The larger equilibrium values reached at α^* in the tactics not inherited case are only sensible if the increased population is not limited by food resource availability. A next step would be to include a limiting term in the model. For instance $\left(1 - \frac{S+bP}{K}\right)$ where b = (mass of parentals)/(mass of sneakers) to account for the difference in consumption of the two differently sized males, and K is overall food resource carrying capacity for the system.

Another simplification in our model that merits future consideration is that we have only considered the adult (sexually mature) stage. To properly represent the juvenile stage, a time delay should be added. This addition becomes more important if one property of the alternative tactic is earlier (or delayed) maturation; in such a scenario, we would be interested in testing the effects of having separate time delays for each phenotype.

In our model we have assumed that tactic is fixed (e.g., individuals will either sneak or provide parental care once they mature, and will do so for life). However, ARTs can also be performed sequentially, or even change multiple times. Sequential ARTs may be most optimal in species, such as fish, with indeterminate growth (Oliveira et al., 2008). For instance, if the choice to sneak or parent is determined entirely by relative size, then round gobies could sneak when they are small and switch to parenting when they become large enough to compete with other parental males. This has been shown to be the case in the common goby (*Pomatoschistus microps*; Magnhagen, 1992. A term representing the switching of sneaker male to parental male, possibly dependent upon density, could be incorporated into this model.

Finally, our models assumed two extreme cases of heritability of tactics. Many tactics, however, cannot be classified as either fully inherited, or controlled entirely by environmental factors (Lucas and Howard, 2008). An obvious modification of the model would be to allow partial inheritance of tactics (i.e., offspring express the same tactic as their parent with a certain probability).

Alternative reproductive tactics have the potential to drastically change the dynamics of a population. The type and magnitude of these changes is further dependent upon causal mechanisms of ARTs, such as heritability. It is therefore crucial that ARTs be incorporated when modelling populations, and that the mechanism determining the expression of an ART in the focal species is determined. Our results have shown that perturbations in the rates of change of a population (by increasing their mortality, for instance) can have unexpected consequences on the population. The consideration of ARTs is therefore of an even greater importance when evaluating policy for conservation or for commercial harvest of a species in which there is more than one reproductive strategy.

7 Appendices

A Stability of the extinction equilibrium (tactic not inherited)

To determine the stability of the fish free equilibrium (i.e. whether the population will tend toward zero and crash, or away from zero toward a positive value) we must evaluate the derivative of (8) with respect to F at $F = 0$. We find that the fish free equilibrium is stable when

$$\alpha > 1 - \frac{1}{L_{\mathrm{p}} \cdot W(A)} \tag{14a}$$

where

$$A = \frac{\nu_{\mathrm{p}}}{\mu L_{\mathrm{p}}} \exp\left(\frac{1}{L_{\mathrm{p}}}\right) \tag{14b}$$

and W is Lambert's W function (Weisstein). If $\mu \geq \nu_{\mathrm{p}}$ then $A \leq \frac{1}{L_{\mathrm{p}}} \exp\left(\frac{1}{L_{\mathrm{p}}}\right)$. Since $W(x)$ is monotonically increasing, $W(A) \leq W\left(\frac{1}{L_{\mathrm{p}}} \exp\left(\frac{1}{L_{\mathrm{p}}}\right)\right)$. Also, $W(xe^x) = x$ (by definition of inverses), so $W(A) \leq 1/L_{\mathrm{p}}$. Hence the RHS of inequality (14a) is negative, implying that $F = 0$ is stable for any $\alpha \in [0, 1]$, in this circumstance.

Otherwise, the critical $\alpha > 0$. Since $A > 0$ (for all non-zero parameter values), then $W(A) > 0$ also, implying that α lies within $(0, 1)$. Note that this point of change in stability is independent of the parameters ν_{s}, K_{p}, L_{s}, and m_{s} (see Table 1 for parameter definitions).

B Stability of non-zero equilibria $F_\pm$ (tactic not inherited)

Since we are considering a one-dimensional system, global stability is completely determined by local stability of the equilibria. We know that there are at most three equilibria. We determined the stability of the first equilibrium, $F = 0$, in Appendix A. While the expression for $F_\pm$ is too unwieldy to determine the stability of these points directly, we can still accomplish this by assessing the sign of equation (8) for F values around these equilibria.

Consider first the sign of equation (8) in the limit as $F \to \infty$. The first term of (8) is negative whenever $F > K_\mathrm{p}/(1-\alpha)$ and its magnitude is unbounded as F increases. The second term is bounded because $f(P) \leq m$ and the third term is constant and negative. Consequently, regardless of parameter values, $dF/dt < 0$ for all sufficiently large F, and all populations greater than the largest equilibrium value will decline.

Claim 1 $\alpha < \alpha_\mathrm{crit} \Rightarrow F_- < 0$ *and* $F_+ > 0$, *where* α_crit *is the critical value in expression* (14a), *derived in Appendix A, at which the stability of* $F = 0$ *changes.*

Suppose

$$\alpha < \alpha_\mathrm{crit} = 1 - \frac{1}{L_\mathrm{p} \cdot W(A)} \tag{15a}$$

(where W is Lambert's W function (Weisstein) and A is as defined in Appendix A). Then $F = 0$ is unstable (by Appendix A). We also have the following:

$$\frac{1}{1-\alpha} < L_\mathrm{p} \cdot W(A), \tag{15b}$$

and

$$\frac{\alpha}{1-\alpha} < L_\mathrm{p} \cdot W(A) - 1 \tag{15c}$$

Looking at the expression for the non-zero equilibria, $F_\pm$ (9a), we see that if $ME < 1$ then the square root term in this expression will be real and larger than $K_\mathrm{p}B$. Thus, F_- will be negative, and F_+ positive. We show below that the above supposition implies that $ME < 1$. Note for step (16d) that $W(x)e^{W(x)} = x$ (by property of inverses).

$$
\begin{aligned}
ME &= \frac{\mu}{\nu_\mathrm{p}(1-\alpha)} \exp\left(\frac{\alpha}{L_\mathrm{p}(1-\alpha)}\right) && \text{(16a)} \\
&< \frac{\mu}{\nu_\mathrm{p}} L_\mathrm{p} \cdot W(A) \cdot e^{\frac{1}{L_\mathrm{p}}(L_\mathrm{p} \cdot W(A) - 1)} && \text{(16b)} \\
&= \frac{\mu}{\nu_\mathrm{p}} L_\mathrm{p} \cdot W(A) \cdot e^{(W(A) - 1/L_\mathrm{p})} && \text{(16c)} \\
&= \frac{\mu}{\nu_\mathrm{p}} L_\mathrm{p} \cdot A \cdot e^{(-1/L_\mathrm{p})} && \text{(16d)} \\
&= \frac{\mu}{\nu_\mathrm{p}} L_\mathrm{p} \left(\frac{\nu_\mathrm{p}}{\mu_\mathrm{p} L_\mathrm{p}} e^{1/L_\mathrm{p}}\right) \cdot e^{(-1/L_\mathrm{p})} && \text{(16e)} \\
&= 1 && \text{(16f)}
\end{aligned}
$$

We therefore have that if $\alpha < \alpha_\mathrm{crit}$, then $F = 0$ is unstable (and so dF/dt is positive for small F), and $F_+ > 0$ by Claim 1. We also have that $dF/dt < 0$ for large F, which implies that F_+ is stable. This proves the Case 2 (certain persistence) in section 4.2.1.

Following a similar proof for the claim above, we see that if $\alpha > \alpha_\mathrm{crit}$ (and so $F = 0$ is stable), then $ME > 1$, and there are three possibilities for the configuration of $F_\pm$.

(a) **$F_\pm$ are complex:** Since this implies only one equilibrium ($F = 0$), and $dF/dt < 0$ for large F, then the extinction equilibrium is stable (Section 4.2.1: Case 1, certain extinction).

(b) **$F_- \leq F_+ < 0$:** This happens when, in addition to the criteria for α, B from expression (9a) is positive. This case is the same as the previous case with no positive equilibria, resulting in a stable zero equilibrium (also Case 1, certain extinction).

(c) **$0 < F_- \leq F_+$:** This happens when $B < 0$. Again, we know that $F = 0$ is unstable, and $dF/dt < 0$ for sufficiently large F. Consider F_+ strictly greater than F_-. Given this information, and the fact that there are at most two non-zero equilibria, there are two possibilities for the stability of $F_\pm$: F_- is unstable and F_+ is stable, or both points are semi-stable (with $dF/dt \leq 0$ for all $F \geq 0$). Supposing that the latter scenario were true, this would require that the function dF/dt have four critical points. However, if we take the partial derivative of dF/dt with respect to F, and clear the denominator, we find that the resulting polynomial is of degree 3, and therefore has at most

3 solutions, implying that dF/dt has at most 3 critical points. Thus, we must have that F_- is unstable, and F_+ is stable (Section 4.2.1: Case 3, Allee effect). Consider, finally, the special case where $F_+ = F_-$. By continuity of dF/dt (with respect to F), and the fact that there are at most 2 non-zero equilibria (and, again, that $dF/dt < 0$ for large F), this point $F_\pm$ must be semi stable; all populations larger than $F_\pm$ will tend to this point, and all others will tend to zero.

C Parameter ranges for global sensitivity analysis

To perform global sensitivity analysis we must first determine ranges from which each parameter will be chosen. When data are available for the estimation of parameters, confidence intervals from these estimates can be used as input ranges for sensitivity analysis (Ellner and Guckenheimer, 2006). In the absence of proper estimations, we make a best guess from the relevant literature.

Parameter ranges for this analysis have been chosen as follows, with parameters chosen uniformly from these ranges for analysis (see Table 2 for a summary). We allow the proportion of sneakers to be between 0 and 0.95 (to avoid dividing by zero). Adult round gobies live up to four years, and mature as early as 1 year (Corkum et al., 1998). We therefore consider breeding lifespans in the range from 1 to 3 years, which gives mortality rates (μ) in the range $[1/1 = 1,\ 1/3 = .33]$. Survival rates of young round gobies are unknown (MacInnis and Corkum, 2000), and so we consider ν_s and ν_p (intrinsic reproductive rates of parental and sneaker males, and subsequent survival to maturity) from the same ranges as mortality rates. We also explore as a separate case when the ranges of these rates exceed mortality rates (ν_p and ν_s from $[1.33, 2]$).

In the common goby (*Pomatoschistus microps*), Borg et al. (2002) found experimentally up to three sneakers visiting one parental nest at once. Similarly, Jones et al. (2001) found genetic evidence of fertilization from up to five additional males in one nest in the sand goby (*Pomatoschistus minutus*). In lieu of similar estimates for the round goby, we use these as a basis for the range of values for parental resisance to sneakers (L_p), as well as sneaker limit per parental (L_s); we assess both of these parameters in the range $[1,\ 10]$. Finally, since maximum sneaker visits (m_s) is, to our knowledge, unestimated, we choose m from [1.1, 10] (to avoid dividing by zero). Finally, the range for parental breeding space capacity K_p is set to be from $[20 - 25]$. This low capacity is chosen to make the results easier to see in a plot (i.e., so curves are separated sufficiently to distinguish differences). Results did not differ appreciably at larger carrying capacities.

D Global sensitivity analysis

It is impossible to completely understand how different parameter values will influence the model output through local analysis alone. With global sensitivity analysis (SA), however, we can vary all parameters simultaneously to get an overall sense of parameter influence. This appendix describes the methods used to perform a global stability analysis, which assesses the strength and direction of influence that each parameter value has on the model output of interest (See sections 4.3 and 5.2.3 for results).

For this analysis, multiple sets of parameter values are chosen from predetermined ranges (see Appendix C) and distributions (uniform, in our case). These sets are treated as "experimental data" that are then used as input values for the model. The output values then become "observations", and statistical analyses are conducted on this data (Ellner and Guckenheimer, 2006). In this paper we use two statistical methods.

We first fit the data with a multiple linear regression model and use standardized regression coefficients (SRCs) to determine the direction of influence for each parameter (i.e., if we increase the parameter value, would we expect an increase or decrease in the equilibrium population; Saltelli et al., 1999; Ellner and Guckenheimer, 2006). If the relationship between parameter and model output is strongly linear, then standardized regression coefficients are meaningful, but can otherwise be misleading if the true relationship is quadratic, or of a higher order (Ellner and Guckenheimer, 2006). Since our model is non-linear, we limit the interpretation of these coefficients to qualitative description.

To quantify the relative magnitude of influence that each parameter has on the model output, we use a variance decomposition technique called (extended) Fourier Amplitude Sensitivity Test (FAST; described in Saltelli et al., 1999, computations completed using the R package "Sensitivity", (Pujol, 2008)). Alternative methods can be seen in Sobol' (2001). This method uses

Fourier transforms to define a search curve which then chooses a representative sample of parameter sets at which to evaluate the model output (Saltelli et al., 1999). Similar to an ANOVA, the FAST method then estimates how much of the output variance can be attributed to each parameter (or factor), and provides both the main effect and the total effect (main effect plus interactions) for each parameter.

The main effect index (M_i) estimates the following quantity:

$$M_i = \frac{\mathrm{V}_{\mathrm{X}_i}[E_{X_{-i}}(Y|X_i)]}{\mathrm{V(Y)}} \tag{17}$$

where X_i represents input factor of interest, X_{-i} the remaining factors, and Y the model output. Variance in the output is estimated over all values of parameter X_i, holding each value constant while the X_{-i} are varied. This index tells us by what proportion the variance in the output would be reduced if the parameter in question were known.

The total index (T_i) estimates the following:

$$T_i = 1 - \frac{\mathrm{V}_{\mathrm{X}_{-i}}(E_{X_i}(Y|X_{-i}))}{\mathrm{V(Y)}}. \tag{18}$$

This index gives the fraction of variance that would be *left* if all other factors were fixed. We can use this index for parameter reduction; factors with a low total index can be fixed at any value in the assessed range without significantly reducing the variance in the model output (Saltelli et al., 2004).

E Uniqueness of the non-zero equilibrium (Tactic inherited)

In this section we make an argument that, in the tactic inherited model (10), there is at most one equilibrium where both sneaker (S) and parental (P) populations are positive. We do so by proposing that the associated nullclines (13) cross at most once in the positive quadrant.

First consider the nullcline derived from $dP/dt = 0$ (13a). Evaluating this expression at $P = 0$ we find that the curve crosses the S-axis only once at

$$S = -\ln \mu_{\mathrm{p}}/\nu_{\mathrm{p}} \tag{19a}$$

which is positive when $\mu_\text{p} < \nu_\text{p}$. The curve crosses the P-axis twice, at

$$P = -1/L_\text{p}, \quad P = K_\text{p}(1 - \mu_\text{p}/\nu_\text{p}). \tag{19b}$$

The first point is always negative, and the second is positive when $\mu_\text{p} < \nu_\text{p}$. The curve must go through both of these positive points. Furthermore, it has only one critical point, and is concave down whenever $P < 2K_\text{p} + 1/L_\text{p}$. Since P is not defined, for $P > K_\text{p}$, the curve is concave down for all of its domain.

Next consider the nullcline derived from $dS/dt = 0$ (13b). This curve crosses the P axis at

$$P = -1/L_\text{s}, \quad P = \mu_\text{s}(m_\text{s} - 1)/(\nu_\text{s} m_\text{s} - \mu_\text{s}). \tag{19c}$$

Since it is undefined at $P = 0$, we are only interested in the latter of these two points, which is positive whenever $m_\text{s} > \mu_\text{s}/\nu_\text{s}$ (since $m_\text{s} > 1$). When $P > 0$ this curve is concave down, and its only critical points are at

$$P = \sqrt{\frac{-\mu_\text{s}(m_\text{s} - 1)}{L_\text{s}(\nu_\text{s} m_\text{s} - \mu_\text{s})}} \tag{19d}$$

These points are real only when $m_\text{s} < \mu_\text{s}/\nu_\text{s}$ (the opposite criterion for having the nullcline cross the axis at a positive P-value), and so there are no critical points in the positive quadrant. In addition, we have that the nullcline approaches $-\infty$ as P approaches 0. Since it is also both concave down and lacking critical points (for positive P), the nullcline is monotonically increasing.

Given these conditions, if the second nullcline crosses the P-axis at P greater than the sneaker-free equilibrium ($P = K_\text{p}(1 - \mu_\text{p}/\nu_\text{p})$), there will be no non-zero equilibria (i.e., there will be only the extinction and the sneaker-free equilibria). If the second nullcline crosses at P less than the sneaker-free equilibrium, it will cross the first nullcline at least once (i.e., at least one equilibria). Suppose that the nullclines were to cross twice (i.e., the second nullcline crosses outside of the first, and then back in). Since both curves are concave down, and since the second exists for all $P > 0$ (while the first does not), the nullclines would need to cross a third time. However, from expression (10b) we see that there are at most two distinct equilibrium values for S (thus ruling out two crossing points). In order to cross more than three times, one of the nullclines would need to have an additional critical point. Thus, there is at most one point where the nullclines cross in the positive quadrant, and at most one positive equilibrium with non-zero parental and sneaker populations. Furthermore, this point will be present whenever the second nullcline crosses the P-axis at a value below the sneaker-free equilibrium.

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4 Conclusions and summary of future needs

The two parts of this thesis investigated factors influencing the dynamics of an invasive fish population in the Great Lakes. Both studies suggest many directions for future research that would contribute to our understanding of round goby dynamics, and also to control and management strategies

4.1 Part I: Empirical observations

Part I of the thesis summarized seven years of data on the abundance, size and sexes of round gobies in Hamilton Harbour, and explored patterns over time, season and habitats (substrate types). While we provide conjecture regarding the causes for these observed patterns, evidence supporting these conjectures is largely circumstantial and requires further study. Below, I outline some of the questions this study raised.

Why has the population declined over time? We hypothesized that this may be a result of increased predation on the round goby, or a decrease in a previously abundant food supply. This could be tested by correlating the abundance of predator and of prey of the round goby.

Why are gobies getting smaller? We found that the average size of round gobies has decreased along with abundance. We hypothesize that this decline may be correlated with an increase in the relative numbers of a newly observed non-conventional male phenotype (the sneaker male). The presence of this alternative male reproductive tactic may be driving the median size of gobies down. However, as sneakers have only been recorded since 2006, this hypothesis cannot, as yet, be confirmed. Studies to determine the age of maturation of both male types are currently underway, the results of which may contribute to the understanding of size trends.

Seasonality and Catchability of round gobies. Our results suggest that the abundance of round gobies is related to water temperature. However, it may be that this factor is affecting the catchability of round gobies (whether or not they swim into a trap) rather than their actual abundance. Future studies could investigate how round goby movement correlates with water temperature. Additionally, data from traps set in deeper waters (and the associated water temperatures) could be compared; it could be that gobies are merely moving to more favourable waters in extreme temperatures.

Substrate affinity. We found gobies on mud, which was previously thought to be resistant to the species. We also found gobies (albeit in much smaller numbers) in Cootes Paradise Marsh, which contains muddy substrate. We conclude that mud is not excluding round gobies from the wetlands, but that there may be some other factor preventing the level of establishment that we observed in Hamilton Harbour. An understanding of any such factors is important for keeping this invasive species out of this and other similar wetlands. Also of interest is how gobies are able to survive in mud; these habitats lack the structurally complex structures that are thought to be preferred for breeding. One hypothesis for future study is that the increased turbidity (reduced clarity) on muddy substrates may improve the ability of round gobies to evade predators, partially compensating for the lack for breeding structures.

4.2 Part II: Theoretical analysis

Part II investigated the affects of alternative reproductive tactics on population dynamics through mathematical models. We found that the presence of two competing male phenotypes drastically changed the population size and the population dynamics. Both of these factors are further influenced by whether or not it is assumed that tactics are inherited. As with part I, this study suggests future experiments involving alternative reproductive tactics, and also suggests caution when considering conservation or commercial policy.

Unexpected population increases. In the first model, where tactics are not inherited, we found that a decrease in the reproductive success of parental males could result in an *increaese* in population size. Similarly, in the model where tactics are inherited, decreasing the reproductive success of sneaker males can result in a larger population. In other words, harvesting parental or sneaker males (depending on whether tactics are inherited or not inherited) could actually increase the population; such possibilities should be considered in management and control strategies, and in recreational and commercial fishing policy pertaining to the round goby.

Oscillating populations A further consideration for the harvesting of round gobies is that an increase in parental mortality can have a destabilizing effect, and lead to a stable cycle (continuously, regularly fluctuating populations). If the tactics inherited model is appropriate, the observation of oscillating populations could mean one of two things; either the population is exhibiting damped oscillation toward an equilibrium (stable population size), or that parameter values are such that the population is in a stable cycle.

Limitations of parameter estimation. Better estimates of model parameters for the population in question are now needed to narrow down the set of plausible dynamics. Necessary parameter estimates include: intrinsic reproductive rate of both male phenotypes, as well as the survival of their young to maturity; mortality rate; nest space; a measure of the reduction in parental reproductive output as a result of sneakers; the maximum number of sneakers per nest before sneaker reproductive output is affected; and the number of nests a sneaker can visit/fertilize per unit time. While we examined a plausible set of these parameters based on literature on similar species with ARTs, experimental estimates of the focal population would provide more meaningful results.

Given such estimates, and the resulting set of plausible dynamics (as predicted by the model), we could then engage in a more meaningful sensitivity analysis (using the confidence intervals of these estimates as parameter ranges). From this we could determine which parameters are most important in determining changes in the various model output values (equilibrium population size, threshold for persistence, or amplitude/frequency of oscillation). We would then know which parameters should be more accurately estimated, and also which parameters should be targeted for control or management strategy.

In general, our modelling shows that alternative reproductive tactics can strongly influence population dynamics, and should be considered whenever studying the population ecology and biology, and the impacts of such, in a species in which ARTs are present.

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