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Accounting for variability in life-history traits for the definition of amphidromous goby fry fisheries closure periods

by

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Abstract. – Amphidromous goby fry (post-larvae and young juveniles) are traditionally fished when they arrive in rivers after their larval development at sea. In Reunion Island (Indian Ocean) two species of amphidromous goby are mainly targeted by the fisheries: the endemic *Cotylopus acutipinnis* and the cosmopolitan *Sicyopterus lagocephalus*. Despite the lack of quantitative data on these fisheries, their impact on populations is expected to be important because the catches can represent several tonnes per year. Consequently, fishery regulation changes have been proposed that increase the duration of the existing fisheries closure period of two weeks in March. We developed an approach to identify key periods for fisheries closure, including assessment of the proposed management scenario and several alternative protection scenarios, based on the maximization of fry abundance and on the variability of four life-history traits: (i) fry size and (ii) age at arrival in rivers, (iii) the time the juveniles spend in river before maturation and (iv) their migration behaviour. This approach is in seeking to preserve a high level of phenotypic diversity, which is predicted to promote population resilience. We conducted a multiple-criteria decision analysis to rank 4096 alternatives of fisheries closure periods, ranging from zero to 12 months, based on their propensity to maintain fry abundance and life history trait diversity. Finally, according to the type of fisheries closure period (discontinuous or continuous) and the proportion of annual abundance and variability of life-history traits preserved during the period (50% or 75%), we propose four different fisheries closures lasting from six to nine months.

Résumé. – Prise en compte de la variabilité des traits phénotypiques dans la définition d'une période de fermeture des pêcheries d'alevins de gobies amphidromes.

Les alevins (post-larves et jeunes juvéniles) de gobies amphidromes sont traditionnellement pêchés lorsqu'ils arrivent en rivière après leur phase de développement larvaire marine. Sur l'île de La Réunion (océan Indien), les pêcheries ciblent principalement deux espèces de gobies amphidromes : une espèce endémique, *Cotylopus acutipinnis,* et une cosmopolite, *Sicyopterus lagocephalus*. Malgré l'absence de données précises sur les quantités d'alevins pêchés, les captures sont estimées à plusieurs tonnes par an, ce qui laisse supposer un impact important des pêcheries sur les populations. Par conséquent, les autorités locales ont eu pour projet d'allonger la durée de fermeture des pêcheries, qui était jusqu'alors de deux semaines au mois de mars. Afin d'aider les autorités locales dans leur démarche, nous avons mis au point une méthode permettant d'identifier les périodes clés de fermeture des pêcheries. Cette méthode est basée sur la maximalisation de l'abondance d'alevins ainsi que de quatre de leurs traits d'histoire de vie : (i) la taille et (ii) l'âge des alevins à leur arrivée en rivière, (iii) le temps que passent les juvéniles en rivière avant d'atteindre leur maturité sexuelle et (iv) le comportement de migration de ces mêmes juvéniles. Cette approche vise à préserver une diversité de traits phénotypiques élevée, ce qui est sensé améliorer la résilience des populations. Nous avons réalisé une analyse multicritères afin de classer 4096 alternatives de fermeture des pêcheries dont la durée variait entre zéro et 12 mois. Les alternatives étaient classées à partir de l'abondance et de la diversité des traits d'histoire de vie des alevins qu'elles permettaient de garantir. Enfin, quatre périodes de fermeture des pêcheries ont été proposées en fonction du type de période de fermeture (continue ou discontinue) et de la proportion de l'abondance annuelle et de la variabilité des traits d'histoire de vie préservée au minimum pendant cette période (50% ou 75%). Les périodes de fermeture des pêcheries proposées s'étendaient de six à neuf mois.

INTRODUCTION

Fisheries are known to impact fish populations in terms of overall abundance and size structure (Hutchings, 2000) through to species evolutionary responses (Law, 2000; Kuparinen and Merilä, 2007). The removal of individuals by the fisheries has direct impact on the targeted population by reducing the number of spawning adults at each generation (van Gemert and Andersen, 2018). Beyond this direct impact, fisheries can also reduce the phenotypic diversity

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of populations due to fisheries induced selective mortality (Mollet *et al.*, 2007). The reduction of phenotypic diversity can profoundly affect the population dynamic as a population with more diverse phenotypes is expected to be more resilient to unpredicted disturbances than a population with homogenous phenotypes (Moore *et al.*, 2010; Schindler *et al.*, 2015). While specific phenotypes or life-history traits can provide competitive advantages in a definite environmental context, they can appear detrimental in another one. Accordingly, high phenotypic diversity maximises population level adaption to environmental fluctuations, whereas the homogenization of phenotype diversity due to fisheries can increase threat of extinction risk (Heino *et al.*, 1997).

Several fisheries regulations can be applied to limit the effect of fishing on fish populations. These regulations include limiting the catches (quotas), constraining the fishing effort (number of fishers and their time spent fishing) or controlling the methods, periods and location of fishing (Sigurðardóttir *et al.*, 2015). The efficiency of different fishing regulations on the conservation and/or restoration of fish populations has been debated for decades in the scientific community (Villasante *et al.*, 2011). However, successful examples of fisheries regulations typically have a firm scientific basis supported by independent fishery monitoring and some level of acceptance of regulation by the fishers (Beddington *et al.*, 2007).

Amphidromous goby fisheries exist in many locations in the Pacific and Indian oceans (Bell, 1999; Shiao *et al.*, 2015; Nurjirana *et al.*, 2022). These fisheries usually target the post larval and/or juvenile (Keith *et al.*, 2008) stages (referred to as fry hereafter) which return to freshwater to grow (Teichert *et al.*, 2014a), mature and reproduce (Teichert *et al.*, 2014b, 2016a), after a larval growing period at sea (Hoareau *et al.*, 2007). Fisheries directly impact the abundance of fry entering the rivers. Annual catch reported in some amphidromous goby fry fisheries can easily reach tonnes or tens of tonnes of fry (Hoareau, 2005; Shiao *et al.*, 2015). Beyond the direct impact on fish abundance, fisheries can also have indirect impacts on amphidromous goby phenotypes. For example, the fishing gears can be selective for a given fish size, with mesh nets usually retaining large fish with deep bodies. Consequently, the fisheries can impose a selective pressure on the phenotype of fry arriving in rivers by skewing their size distribution, as reported for other commercially exploited species (Olsen *et al.*, 2004; Mollet *et al.*, 2007). When fishing is concentrated within a restricted period, the fishing pressure can result in an over exploitation of the fry phenotypes arriving in rivers during the fishing period, whereas phenotypes of the cohorts outside of this period remain unaffected. This observation is particularly relevant in tropical and sub-tropical areas where amphidromous goby fry can arrive in rivers year round (Bell *et al.*, 1995; Teichert *et al.*, 2012, 2016b). This extended period of fry arrival in rivers is associated with a marked variability of their phenotypic traits. For example, depending on the month of the year that the fry arrive in freshwater, the median size and age of individuals can vary by approximately 15% and 60%, respectively (Teichert *et al.*, 2012, 2016b).

In Reunion Island, the fry of two amphidromous goby species, *Sicyopterus lagocephalus* (Pallas, 1770) and *Cotylopus acutipinnis* (Guichenot, 1863), have been fished for decades (Vaillant, 1890; Aboussouan, 1969). These fisheries have been regulated for years with several measures such as banning collection of fish at sea in the vicinity of river mouths, encouraging use of traditional sampling gears made from vegetal materials, and implanting fisheries closure from the new moon to the full moon of March (approximately two weeks) annually. Fishing quotas are not applicable so far as the fishers are not professional, and there is no obligation to declare their captures. Recently the local authorities enacted a new fishing regulation to manage the goby fry fishery in a more sustainable way. The specific intent is to increase the fishery closure period to protect target species more suitably.

In this context our study provides a method to rank different alternatives of fisheries closure periods, based on several biological criterion aiming at maximizing the abundance and phenotypic variability in *S. lagocephalus* and *C. acutipinnis* populations. The ranking allows a quantitative estimation of the effect of the different fisheries closures to ensure any changes are supported by a strong evidence base to support adoption of changed regulations by fishers.

MATERIAL AND METHODS

General approach

Our approach ranked various fisheries closure periods based on the maximisation of several criteria, including fry abundance and phenotypic diversity. The first step was to define the criteria representative of key life-history stages of *S. lagocephalus* and *C. acutipinnis*. The second step, harnessed available published data to estimate relative abundance and diversity of traits, corresponding to each calendar month, from January to December. These values were then used to assess the monthly contribution to the annual fry abundance and phenotypic diversity. The third step was simulating all the fisheries closures from nil to 12 months in duration. As the fourth step all fisheries closure period scenarios were ranked and evaluated.

Selection of life-history trait criteria

Three criteria representing important stages of the life cycle of *S. lagocephalus* and *C. acutipinnis* were selected (Table I): fry abundance, fry life-history traits and juvenile life-history traits. The first criterion was the abundance of fry arriving in rivers as it directly influences the species popula-

Table I. – Summary of the monthly and yearly value or range (from 2006-2012; min-max, in bracket) of the three criteria of *Sicyopterus lagocephalus* and *Cotylopus acutipinnis* used to rank the alternatives of duration of the fisheries closure periods. "ABD" represents the monthly mean density (± standard error) of fry captured in the mouth of three rivers, "TL" and "PLD" represent the estimated size-at-recruitment and pelagic larval duration of fry, respectively. "MB" represents the tendency of the juveniles to migrate upstream after their arrival in rivers (1: upstream migration, 0: no upstream migration) and "SM" represents the duration spend in river before maturation.

	Criterion	**Life-history traits**	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	**Yearly**
S. lagocephalus	Abundance	ABD (ind.100 m^{-2})	532 ± 111	277 ± 61	411 ± 95	280 ± 66	1133 ± 262	1275 ± 320	2012 ± 886	1063 ± 321	2497 ± 631	1683 ± 488	1445 ± 356	1201 ± 327	13913
	Life-history traits of fry	TL (mm)	(31.8-35.2)	(30.7-35.8)	(29.8-35.3)	(29.0-33.3)	(28.7-32.6)	(28.9-32.4)	(29.5-33.0)	(30.3-3.6)	(30.9-34.1)	(31.3-34.5)	(31.6-34.6)	(31.7-34.6)	(28.7-35.8)
		PLD (days)	(160-231)	(138-260)	(122-253)	(112-211)	(109-161)	(113-145)	(121-159)	(132-178)	(143-196)	(153-211)	(162-227)	(171-242)	(109-260)
	Life-history traits of juveniles	MB (binary)	0	0	0	0	0	0	0	1	1	1	1	0	(0-1)
		SM (days)	(70-98)	(63-112)	(64-125)	(76-135)	(98-138)	(108-134)	(99-126)	(89-117)	(82-108)	(76-102)	(71-97)	(67-92)	(63-138)
C. acutipinnis	Abundance	ABD (ind.100 m^{-2})	125 ± 42	434 ± 146	203 ± 61	278 ± 59	445 ± 133	647 ± 196	525 ± 141	445 ± 146	527 ± 120	357 ± 82	170 ± 56	93 ± 35	4276
	Life-history traits of fry	TL (mm)	(18.6-21.8)	(18.0-21.5)	(17.9-21.0)	(18.3-21.1)	(18.7-21.3)	(19.0-21.5)	(19.4-21.8)	(19.6-22.1)	(19.8-22.4)	(20.0-22.7)	(20.0-22.7)	(20.1-22.6)	(17.9-22.7)
		PLD (days)	(82-134)	(75-121)	(70-106)	(75-106)	(82-111)	(88-119)	(92-128)	(97-137)	(102-145)	(106-150)	(105-154)	(98-157)	(70-157)
	Life-history traits of juveniles	MB (binary)	0	0	0	0	0	0	1	1	1	1	0	0	(0-1)
		SM (days)	(102-123)	(107-127)	(112-129)	(112-127)	(110-123)	(107-120)	(104-118)	(101-116)	(99-114)	(97-112)	(96-113)	(95-116)	(95-129)

tion dynamic (Artzrouni *et al*., 2014; van Gemert and Andersen, 2018). The second criterion was related to the life-history traits of fry upon arrival in rivers, and was reflected by two traits: the pelagic larval duration (PLD) and the size-at-recruitment (total length, TL) of fry. These traits can affect the individual performances for many functional abilities which, in turn, can modulate individual survival in freshwater (Schoenfuss and Blob, 2007; Blob *et al*., 2010). The third criterion was related to the life-history traits of juveniles in freshwater, from arrival in rivers to their first reproduction. These life-history traits can also modulate individuals survival and their likelihood of successfully reproducing (Lagarde, 2018; Diamond *et al*., 2019; Lagarde *et al*., 2020a). Two life-history traits were considered in this third criterion: the propensity of juveniles to migrate toward upstream reaches after their arrival in freshwater (migration phenotype, MP) and the time the juveniles spend in rivers before sexual maturation (sexual maturation, SM).

Estimation of life-history trait variability

The monthly estimates of fry abundance (ABD, ind.100 m^{-2}) arriving in rivers were based on electrofishing data from a monitoring study performed every month, except during a few months due to technical issues, in three river mouths from 2006 to 2012 (ARDA, 2012; Teichert *et al*., 2012, 2016b). Briefly, in each river mouth, a minimum area of 50 m^2 was electro-fished and all individuals were identified to species level. All fry individuals were counted and preserved in 90% ethanol. Other individuals were released on site. The monthly abundances were estimated by the mean abundance (ind.100 m^{-2}) of fry individuals captured in the three river mouths for all years. Finally, the annual fry abundance was estimated by summing the 12 monthly abundances (Table I).

The life-history traits of *S. lagocephalus* and *C. acutipinnis* fry at arrival in rivers were estimated based on the samples collected during the monitoring program described above. The size-at-recruitment (TL) of all fry individuals was measured to the closest mm. A sub-sample of *S. lagocephalus* and *C. acutipinnis* was selected to estimate their PLD based on the interpretation of otolith daily increments formation (Teichert *et al*., 2012, 2016b). For each calendar month, the minimum and maximum values of TL and PLD were estimated with the 5% and 95% quantiles of the raw data to limit the potential influence of outliers. The yearly range of TL and PLD were the minimum and maximum values observed over the 12 calendar months (Table I).

The life-history traits of juveniles were estimated based on previous studies focussing on this life stage (Lagarde *et al*., 2015, 2020a, b). The propensity of juveniles to migrate toward upstream reaches (migration behaviour, MB) was assessed based on the observation of migrating juveniles of *S. lagocephalus* and *C. acutipinnis* in upstream sections (Lagarde *et al*., 2015) and on the duration of migration from the river mouth (Lagarde *et al*., 2020b). For example, most *S. lagocephalus* migrating to upstream reaches are observed from October to January (Lagarde *et al.*, 2015). The duration of migration from the river mouth to upstream reaches was approximately two months for *S. lagocephalus* (Lagarde *et al.*, 2020b). Consequently, most of the *S. lagocephalus* juveniles migrating upstream arrived at the river mouth from August to November. MB was coded as a binary variable for each month: 1 – the juveniles mostly migrate upstream and 0 – the juveniles mostly settle in downstream reaches (Table I). The duration the juveniles spend in river before sexual maturation (sexual maturation, SM) was estimated, for each calendar month, from the minimum and maximum PLD of the fry. Indeed, Lagarde *et al.* (2020a) demonstrated that there is a strong relationship between the PLD of *S. lagocephalus* and *C. acutipinnis* and their SM, with longer PLD associated with shorter SM and vice versa. Consequently, minimum and maximum SM were estimated for each month based on the minimum and maximum PLD. The yearly range of SM were defined as the minimum and maximum values observed over the 12 calendar months (Table I).

Simulation of fisheries closure periods alternatives

The different alternatives of fisheries closures were first identified by enumerating all the possible fisheries closure periods, from zero to 12 months of closure, including continuous and discontinuous periods. The alternatives with continuous periods (*e.g.* December to April) were separated from these with discontinuous periods (*e.g.* December, February and April) because of differences in their acceptability by fishers. Indeed, fishers usually use handmade channels in the river constructed with cobble and gravel to install their fishing gears. These channels necessitate regular and intensive construction and maintenance. Therefore, the discontinuous closure periods result in the fishers needing to construct new channels at the end of each fisheries closure period. This extra work probably makes the discontinuous closure alternatives harder to accept from the fishers compared to continuous period alternatives.

In total, 4096 fisheries closure alternatives were generated, including 134 based on a continuous period and 3962 with discontinuous periods. To evaluate the usefulness of alternatives for preserving abundance and phenotypic diversity, the proportions of the yearly abundance of fry and variability of their life-history traits covered by each alternative were calculated (*i.e.* abundance or maximum variability during the whole period of the alternative / yearly abundance or variability).

Alternatives ranking based on multiple-criteria decision analysis

Finally, all the fisheries closure alternatives were ranked using a Multi-Objective Optimisation on the basis of Ratio Analysis plus the full MULTIplicative form (MULTIMOORA) multivariate analysis. MULTIMOORA allows ranking of alternatives based on multivariate criteria which can be either maximized or minimized (Hafezalkotob *et al.*, 2019). In our study, the best alternative was considered as the alternative for which all the criteria were maximized. It corresponds to a 12-month fisheries closure period, where abundance of fry and diversity of their life-history traits were fully preserved. Conversely, the worst alternative was no fisheries closure period (zero month). The three criteria were weighted identically in the analysis: the fry abundance was given a weight of one, as well as the fry life-history traits (*i.e.* weight of 0.5 for LT and PLD) and juvenile life-history traits (*i.e.* weight of 0.5 for LT and PLD). The MULTIMOORA ranking was performed simultaneously for the two species each species having the same weight in the analysis.

To limit the number of alternatives presented and discussed here, we chose to present only the shortest continuous and discontinuous periods of fisheries closure ensuring preservation of at least 50% or 75%, respectively, of the abundance and life-history trait diversity for each species. The duration and the months included in these shortest fisheries closure periods were identified based on the alternative with the best rank in the MULTIMOORA analysis. All statistical analyses were performed in the R environment (R Core Team, 2018, version 3.5.1), using the MCDM Package (Blanca and Ceballos, 2016) for MULTIMOORA analyses.

RESULTS

Overall, the alternatives with discontinuous fisheries closure periods had higher rank in the MULTIMOORA analysis than the alternatives with continuous fisheries closure periods (Fig. 1). The first 1000 ranked alternatives all included a duration of the fisheries closure period of at least seven months.

The shortest duration of fisheries closure period that preserves at least 50% of the abundance and life-history trait diversity of *S. lagocephalus* and *C. acutipinnis* was six months for discontinuous alternatives (Fig. 2A) and seven months for continuous alternatives (Fig. 2B). When this threshold is increased to 75%, the shortest duration of fisheries closure period was eight months for discontinuous alternatives (Fig. 2A) and nine months for continuous alternatives (Fig. 2B).

The priority months supporting discontinuous fisheries closure for preserving at least 50% of the abundance and diversity in life-history traits of the two species were February, May to August, September and November (Fig. 3). The seven months for the continuous alternative were May to November (Fig. 3). To preserve 75% of the abundance and diversity in life-history traits, the optimum timing of an eight-month closure as a discontinuous alternative was February and May to November (Fig. 3). Similarly, comparable

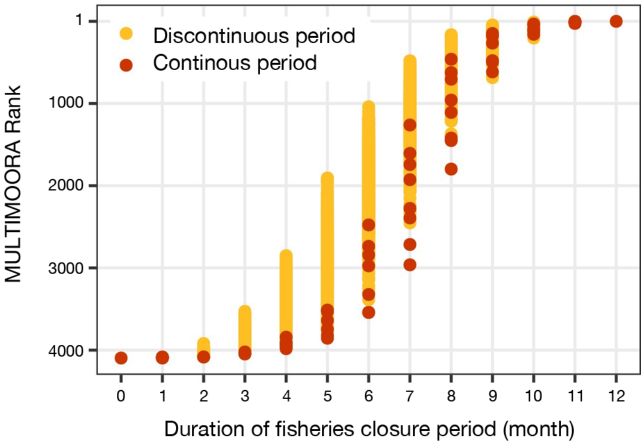

Figure 1. – Ranking of the 4096 alternatives of fisheries closure periods based on the MULTIMOORA analysis on the abundance and life-history traits of *Sicyopterus lagocephalus* and *Cotylopus acutipinnis*. The best alternative is ranked 1 and the worst 4096. Fisheries closure periods are colour coded.

success was forecast with a nine-month continuous alternative spanning February to October (Fig. 3).

DISCUSSION

Our approach which is focused on the phenotypic diversity of *S. lagocephalus* and *C. acutipinnis* presents several advantages in defining an adequate fisheries closure period. The choice of these periods is commonly based on the protection of key stages in the life-cycle of target species, such as migration or reproduction (Munehara *et al*., 2021). However, this method is not applicable for fry fisheries as they target specifically one stage: the fry arriving in rivers. For these fisheries, applying a fisheries closure during the dates of fry arrival in rivers would be equivalent to totally closing the fishery. Accordingly, the fry fisheries closure periods are often defined following fishing quota. For example, the opening date of the European eels (*Anguilla anguilla* L., 1758) fry (glass eels) fisheries is fixed, but the closing date depend on when annual quotas are met (Briand *et al*., 2012). This method is not applicable for goby fry fisheries in Reunion Island because the declaration of the captures is not currently mandatory. Additionally, a fisheries closure period during the main fishing season, which spans from September-October to February (Delacroix and Champeau, 1992), and mainly targets *S. lagocephalus*, would unlikely be accepted by fishers as it would drastically reduce their yearly captures. Our study, based on the maximisation of the abundance and of the variability in key life-history traits, highlights important periods for the conservation of both the endemic *C. acutipinnis* and the cosmopolitan *S. lagocephalus* outside the main fishing season. Indeed, whatever the fisheries closure alternative, the months from May to July and September-October appear pivotal in the conservation of phenotypic diversity for the two species. To a lesser extent the months of February and August highlighted in three of four alternatives also appear relatively important. Except for the months of October, November and February, all the months highlighted in the MULTIMOORA analysis were outside the main fishing season. It will likely make the suggested fisheries closure periods more easily acceptable for fishers. The importance of the May-October period can be explained by the high abundance of both species,

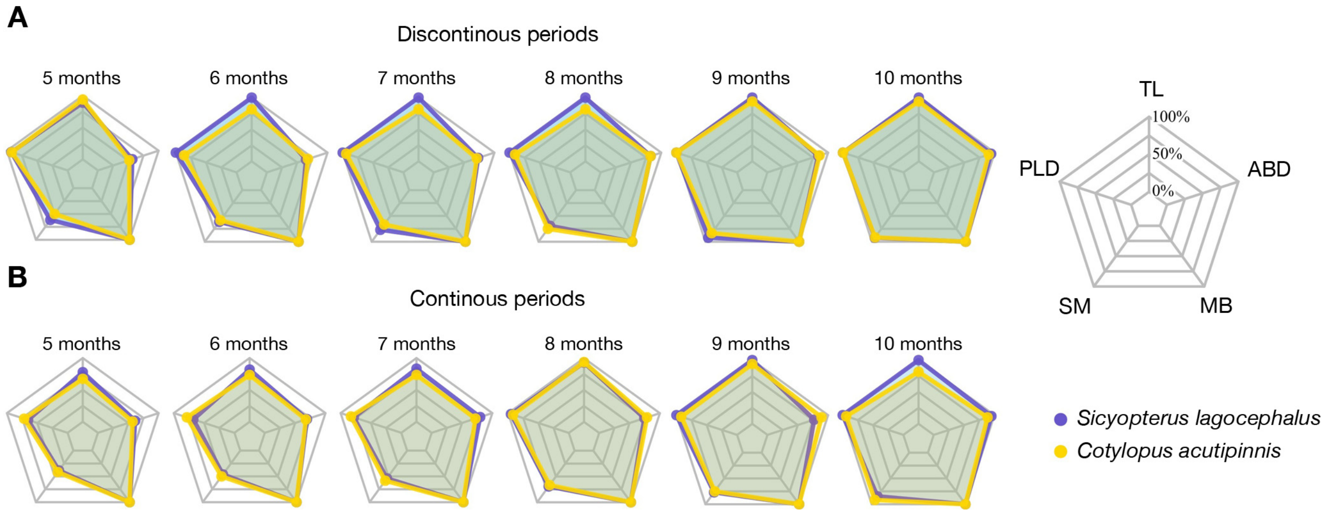

Figure 2. – Proportion of the yearly abundance and variability of life-history traits of *Sicyopterus lagocephalus* (in purple) and *Cotylopus acutipinnis* (in yellow) covered by the best ranked alternatives (with a duration from five to 10 months) of the MULTIMOORA analysis. The best alternatives of discontinuous fisheries closure periods are displayed in panel A, the best alternatives of continuous periods in panel B.

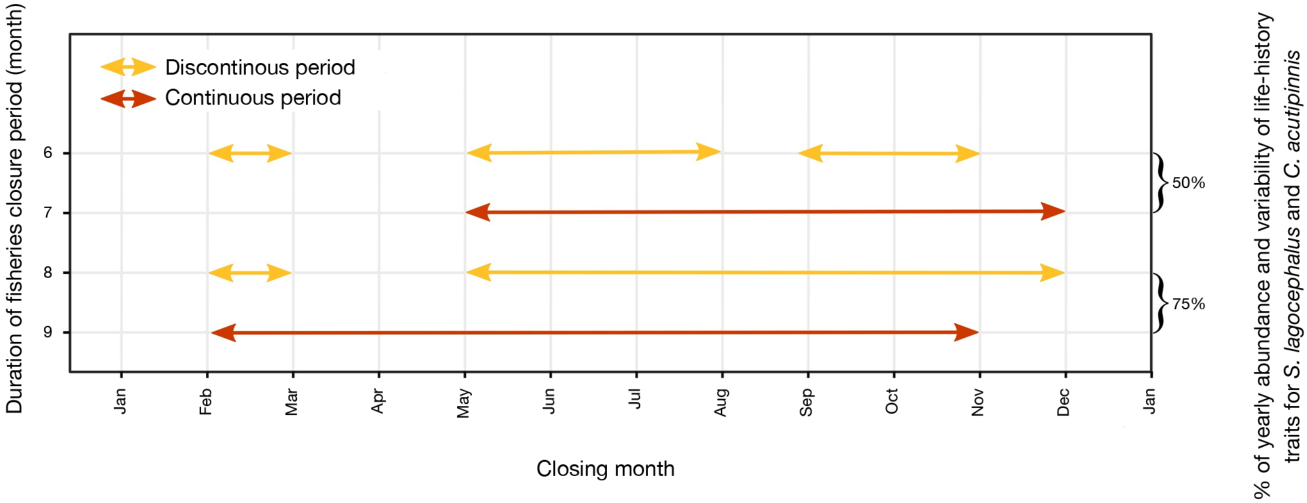

Figure 3. – Representation of the six to nine month fisheries closure periods ensuring that at least 50% and 75% of abundance and life history trait diversity for *Sicyopterus lagocephalus* and *Cotylopus acutipinnis* covered by the discontinuous and continuous alternatives. The months were those selected in the best ranked alternative in the MULTIMOORA analysis.

and especially *C. acutipinnis,* arriving in rivers during these months (ARDA, 2012; Teichert *et al*., 2012). Many other life-history traits such as the TL of *S. lagocephalus*, the SM and MB of both species are also highly variable from May to October (Teichert *et al*., 2012, 2016b; Lagarde *et al*., 2015). The month of February appeared particularly essential for preserving phenotypic diversity, because the PLD and SM of both species and the TL of *C. acutipinnis* were highly variable. In February, the abundance of *C. acutipinnis* fry is among the highest observed for this species. In summary, the fisheries closure periods highlighted in our study enable managers to efficiently preserve the variability of most of the life-history traits for the two species, especially for the endemic *C. acutipinnis*, which is a critical target for biodiversity conservation, while limiting the impact on the main fishing season.

Beyond the advantages described above, our method based on the abundance and on the maximization of phenotypic diversity enables identification of a suitable fisheries closure period that could contribute to enhance the resilience of the fish population to environmental and anthropogenic pressures. The variability of several life-history traits, such as the timing of migration (Moore *et al*., 2010), the habitats used (Tsuboi *et al*., 2020), the size and shape of individuals (Hilborn *et al*., 2003), have often been associated with strong resilience of fish populations to several natural and anthropogenic stresses. In tropical islands, the rivers are often the source of diverse, intense and highly variable (in time and space) selective pressures on fish species (McDowall, 2010). In this context, the maintenance of variability in life-history traits is expected to play a key role in population dynamics, particularly in amphidromous gobies for which trade-offs between phenotypes adapted to opposing selective pressures occur (Blob *et al*., 2010). For example, after their arrival in rivers, amphidromous gobies face the selective pressure of predation, notably within downstream reaches (Diamond *et al*., 2019).

Two strategies allow the amphidromous gobies to limit the risk of predation. First, they can climb waterfalls and/or man-made migration barriers to reach upstream reaches where the predation pressure is limited as only a few, if any, predators can climb waterfalls (Diamond *et al*., 2021; Lagarde *et al*., 2021a). Second, amphidromous gobies can stay in downstream reaches where their survival depends on their capacity to avoid predation. Two studies conducted in Hawaii on *Sicyopterus stimpsoni* (Gill, 1860) and in Reunion Island on *S. lagocephalus* and *C. acutipinnis* demonstrate divergent morphologies between individuals which are either suited to climbing waterfalls else avoiding predators (Blob *et al*., 2010; Lagarde and Ponton, 2023). Consequently, ensuring that variable fry phenotypes colonise the rivers optimizes the likelihood that individuals with different morphologies successfully reach streams and settle there. Furthermore, the relative importance of the two selective pressures can fluctuate among rivers (*i.e*. different abundance of predatory species, characteristics of the first waterfall) and temporally within watersheds (*i.e*. the abundance of predator can be greatly reduced after floods, Smith and Kwak (2015)).

Another important trade-off for amphidromous gobies concerns the time individuals spend at sea (PLD) and the duration they spend in river (SM) before their first reproduction (Lagarde *et al*., 2020a). *Sicyopterus lagocephalus* and *C. acutipinnis* individuals with a longer PLD arrive in rivers at a larger size and can reach their SM earlier than individuals with a shorter PLD. The larger size of individuals with a longer PLD probably also provide a competitive advantage for settlement after they enter rivers. Indeed, male sicydiines gobies have a strong territorial behaviour when they select their spawning habitat (Fitzsimons and Nishimoto, 1990; Teichert *et al*., 2013). Larger individuals are probably more competitive and thus more likely to be able to select an appropriate spawning habitat. Moreover, the earlier SM of individuals with a longer PLD also limits the risk of mortality in freshwater before their first reproduction due to catastrophic events such as cyclonic floods, drought or volcanic eruptions (McDowall, 2010). In contrast, individuals with a longer PLD have a greater risk of mortality during their marine stage due to unpredictable environmental conditions, such as predation, over dispersion or starvation. The relative risk of mortality at sea and in rivers can strongly fluctuate over years in relation to the variability of marine currents, to the occurrence and timing of cyclonic floods, and due to the food availability in both habitats. In this context, the successful colonization of watersheds and the first reproduction of *S. lagocephalus* and *C. acutipinnis* with different PLD and SM may be variable among years. It highlights the value of defining a fisheries closure period which maximizes the variability of phenotypes along this continuum of longer PLD and shorter SM-shorter PLD and longer SM.

As described above, our method for the definition of fisheries closure periods theoretically presents majors advantages in terms of being acceptable to fishers and being sustainable. However, field validation is required. Moreover, the fisheries are not the only anthropogenic pressure threatening populations of amphidromous gobies. As migratory species, amphidromous gobies are directly or indirectly impacted by numerous anthropogenic pressures such as alteration of migration pathways, freshwater and marine habitat degradation, climate change and non-indigenous species (Keith, 2003; Jarvis and Closs, 2019; Pouil and Colsoul, 2021). Consequently, monitoring the response of *S. lagocephalus* and *C. acutipinnis* populations to future fisheries closures is desirable. Ideally, this monitoring should focus on several life-stages of *S. lagocephalus* and *C. acutipinnis*. Particularly, it would be informative to simultaneously survey the abundance of fry arriving in rivers (ARDA, 2012; Boussarie *et al*., 2016), and juveniles and adults which have settled in rivers (Ocea Consult', 2014; Lagarde *et al*., 2021b) and of larvae that drift down to the sea (Lagarde *et al*., 2017, 2018). This simultaneous monitoring could demonstrate the effect of the implementation of a new fisheries closure period and/or highlight other impacts which are likely to overcome the effect of fisheries. For example, if the abundance of fry arriving in rivers increases but the abundances of juveniles and adults settled in rivers and the abundance of larvae that drift down to the sea remain stable, it could be hypothesized that the main impacts that limit *S. lagocephalus* and *C. acutipinnis* population growth are located in freshwater, upstream of the fisheries. Finally, and possibly most important of all, is monitoring socio-economics implications of the implementation of a new fisheries closure period (Thomas, 2017). This is pivotal to better understand the acceptance of the new regulation by the fishers and to support potential adaptation of the regulation (Cambra *et al*., 2021). Such a socio-economics approach would also be an opportunity to communicate in the field with fishers to better explain the effects of the regulation on *S. lagocephalus* and *C. acutipinnis* and encourage a sustainable fishery.

CONCLUSION

Our study provides essential information that has already helped the local authorities to define a six month fisheries closure period, from March to August, in consultation with the fishers (Préfet de la région Réunion, 2021). Even if this period doesn't completely match our recommendations and doesn't ensure at least 50% of the total abundance and variability of all life-history traits for each target species, it overlaps with the most import months for species conservation based on our analyses. Moreover, this period enhances the conservation of the endemic *C. acutipinnis* while maintaining fishing activity for *S. lagocephalus*. Ongoing monitoring of *S. lagocephalus* and *C. acutipinnis* populations will provide information essential to the adaptive management of the fishery.

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