

Ocean warming affects the distribution and abundance of resident fishes by changing their reproductive scope

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Abstract With ocean warming predicted globally, one of the mechanisms driving distributional shifts and changes in the abundance of resident fishes is reproductive output. The relationship between sea surface temperature and the reproductive activity of a eurythermic, resident coastal species, blacktail seabream *Diplodus sargus capensis*, was examined in the “ocean warming” hotspot of the northern Benguela. Reproductive activity was found to be restricted to periods when the water temperature dropped below 20 °C. A metadata analysis conducted on the *D. sargus* sub-species complex similarly showed that reproductive activity was restricted to temperatures between 15 and 20 °C, regardless of the range in ambient water temperature. Based on these findings and using satellite derived SST information, we examined *D. s. capensis*’s total and seasonal “reproductive scope” that is defined as either the area suitable for spawning each year or the duration of its potential spawning season at a fixed geographical locality, respectively. Trends were examined over the last three decades. Reproductive scope by area was found to be shrinking at a rate of 7 % per decade in southern Angola and expanding at a rate of 6 % per

decade in northern Namibia. Reproductive scope by season decreased by 1.05 months per decade in Namibe, southern Angola and increased by 0.76 months per decade in Hentiesbaai, northern Namibia. Changes in reproductive scope may be a driving mechanism of distributional shifts in resident fishes, although the rate of the shifts is likely to be slow. More importantly, changes in reproductive scope will not be uniform throughout fish distributions and will most likely result in heterogeneous variations in fish abundance.

Keywords Angola · Blacktail seabream · Global climate change · Sea surface temperature

Introduction

Although it is accepted that climate change will have a major influence on the marine environment and its biota (Pörtner and Peck 2010), there is a paucity of predictive information on its potential impacts. In fishes, this development of predictive information is complicated by their diverse habitats, physiology and life histories. When coupled with the diverse regional climate variation, population- and area-specific research appears to be a prerequisite for the development of predictive models (McFarlane et al. 2000).

Of all of the climate driven physical and chemical stressors, changes in the ocean temperature is considered to be the most influential with a growing body of

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evidence highlighting its influence on fish distribution patterns (Stebbing et al. 2002; Perry et al. 2005; Last et al. 2011). This is hardly surprising as water temperature changes are known to affect several physiological processes in fishes, including their metabolic rate, fluidity of membranes and organ function (Hochachka and Somero 2002). Water temperature also has a significant influence on nerve, endocrine and reproductive systems (Luksiene and Svedang 1997). Interestingly, despite all of these potential impacts several medium and long-term monitoring studies (Holbrook et al. 1994, Malcolm et al. 2007; Stuart-Smith et al. 2010; James et al. 2012) have indicated that the composition of many coastal fish assemblages has remained relatively stable, despite increases in water temperature. One commonality amongst the abovementioned fish assemblages was that they were dominated by resident species.

Unlike migratory fish species, resident fishes have evolved to be tolerant of fluctuating diel and seasonal temperature regimes and many have therefore developed a broad physiological tolerance to temperature. Pörtner and Knust (2007), using laboratory studies on the eelpout (*Zoarces viviparus*), identified oxygen limitation as the primary mechanism driving thermally induced distributional shifts in fishes. Based on the assumption that this is the primary mechanism, scientists can predict the spatio-temporal distributional patterns of fishes using a combination of respirometry experiments (to determine the upper and lower thermal limits of species) and water temperature forecasting. However, with the evolution of eurythermy in many resident fishes, oxygen limitation may not necessary be a primary mechanism driving shifts, except at the margins of their distribution ranges. In these cases other mechanisms such as changes in reproductive output may drive distributional shifts. For example, reproductive failure in an area that becomes unfavourable, or the successful recruitment of eggs and larvae into a new favourable environment (Figueira et al. 2009) may drive distributional shifts in eurythermic resident species.

Water temperature has a major influence on many aspects of fish reproduction including fecundity and egg size (e.g. Brown et al. 2006), the rate of egg development (Hilder and Pankhurst 2003; Rombough 1997; Taranger and Hansen 1993), gonad maturation (Davies and Hanyu 1986), and the timing (Lobel 1989; Pankhurst and Porter 2003; Sheaves 2006) and

frequency (Hilder and Pankhurst 2003; Pankhurst and Porter 2003) of reproductive activity. Besides water temperature, the timing of reproductive activity can also be influenced by a combination of other ecological drivers as well as physiological and phylogenetic factors, which can operate either through their effect on gametes, larvae, juveniles and/or adults (Sheaves 2006). The timing of reproduction may be geared to minimize egg predation, maximize dispersal, or provide larvae with maximum opportunity to survive in waters with patchy and irregular distribution of food (Shapiro et al. 1988). Reproductive timing in fishes is governed by proximate causal factors which serve to cue gonad development in adult fishes and ultimate causal factors which have developed through natural selection acting on survivorship and recruitment of larvae (Lobel 1989). Water temperature has long been recognised as an important proximate reproductive cue in fishes (Lobel 1989; Shapiro et al. 1988), but may also be an ultimate factor as it plays a role in determining the reproductive episodes (reviewed in Pankhurst and Porter 2003).

The reproduction of commercially important resident species such as those belonging to the families Sparidae, Lutjanidae and Serranidae has been reviewed by several authors (Robertson 1991; Sadovy 1996; Sheaves 2006). Many of the species belonging to these families have adopted a bet-hedging spawning strategy (asynchronous spawning) over an extended season to account for variability in egg and larval survival (Robertson 1991). Water temperature was identified as a major determinant of the spawning season in the Sparidae (Sheaves 2006). However, seasonality amongst the other families was thought to be determined by a complex of variables which are influenced by geography and adult biology (Robertson 1991; Sadovy 1996). Water temperature was identified as a potential factor influencing spawning periodicity and Sadovy (1996) concluded that the approximate spawning temperature range of resident reef fishes (excluding sparids) is generally narrower (2–3°) in many tropical regions, when compared with more temperate habitats.

With clear relationships between temperature and spawning periodicity, it follows that ocean warming may alter the reproductive scope of resident fishes, which could in turn, result in distributional shifts. Reproductive scope in this manuscript is defined as the “breadth” of opportunity for reproduction and is

determined as the area and time with suitable environmental and biological conditions including *inter alia* temperature, photoperiod, pH, nutrient availability and access to mates, for spawning. It is a multidimensional index that includes time, space and the importance of any specific spatial, temporal or environmental variable can be easily investigated by integrating the index over all other variables. For example, given a temperature range suitable for spawning by a particular species, the total area suitable for spawning can be estimated by simply integrating over months of the year. Alternatively by integrating over area, the time suitable for spawning during a calendar year can be determined. From a water temperature perspective, ocean warming hotspots provide ideal observatories for the investigation of the impacts of warming on the reproductive scope of fishes. These areas, characterised by above average ocean warming, have been identified in many areas including the northern Benguela (Monteiro et al. 2008) and eastern Australia (Byrne et al. 2009), and the response of organisms could provide predictive information for areas that are warming at normal rates.

The *Diplodus sargus* sub-species complex inhabits the shallow areas (<20 m depth) of the continental shelf in the warm-temperate waters of the Mediterranean, Northeast Atlantic, Southeast Atlantic, Southwest Atlantic, and Western Indian Ocean. The complex is economically valuable to the inshore recreational (Pradervand 2004; Mann and Buxton 1992), subsistence (Richardson et al. 2011a), artisanal (Pajuelo and Lorenzo 2002) and commercial fisheries (Morales-Nin et al. 2005). Like most sparids, this complex is reef associated and displays highly resident behaviour (Erzini and Abecasis 2009; D'Anna et al. 2011; Watt-Pringle 2009). Members of the complex have been described as rudimentary (Richardson et al. 2011b) and protandrous hermaphrodites (Mann and Buxton 1998) suggesting that they demonstrate some flexibility in their reproductive style. Despite this flexibility, all sub-species are asynchronous spawners, have protracted reproductive seasons (up to 5 months) during which they spawn regularly, even daily and consequently have a high annual egg production (Mylonas et al. 2011). After spawning in shallow waters (<6.0 m depth, Richardson 2010), the buoyant, pelagic eggs of species in this complex hatch after 50 to 90 h depending on ambient temperature (Divanach et al. 1982), and larvae remain pelagic for between

14–17 days (Di Franco et al. 2012). Larval dispersal is thought to be relatively wide (100–200 km scale) and post-settlement dispersal of at least 30 km was also observed (Di Franco et al. 2012). There is no information on the thermal tolerance of their eggs and larvae.

This study aims to assess the impact of ocean warming in the northern Benguela “hotspot” on the reproductive scope of an economically important coastal resident fish species *D. s. capensis*. Specifically, the objectives were to investigate the relationship between the water temperature in the well mixed shallow waters (<6.0 m depth) and reproductive activity in southern Angola, conduct a metadata analysis on the relationship between water temperature and reproductive activity within the *D. sargus* complex, and use these data to understand the recent trends in the distribution and duration of suitable thermal conditions throughout their northern Benguela distribution. The findings of the study are then discussed in the context of resident species worldwide.

Materials and methods

Sampling

Sampling was conducted between April 2008 and March 2009 in southern Angola between the towns of Namibe and Tômbua (Fig. 1). Between 29 and 61 adult fish were collected monthly by shallow water spearfishing (<6.0 m depth), hook-and-line techniques from the shore, or purchased from local markets. Each fish was measured (1 mm) (fork length), weighed (whole and without viscera) (0.1 g), and sexed. The gonads were weighed (0.1 g) and the state of gonad maturation was assessed macroscopically (Table 1). Sea surface temperature (SST) was measured daily in situ, whenever possible, for the duration of the study.

Data analysis

Reproductive seasonality was investigated by comparing both the proportion of female fish with ripe gonads (Table 1) in each monthly sample, and by examining peaks in the mean monthly female gonadosomatic index (GSI). A non-linear step model was used to examine the relationship between the

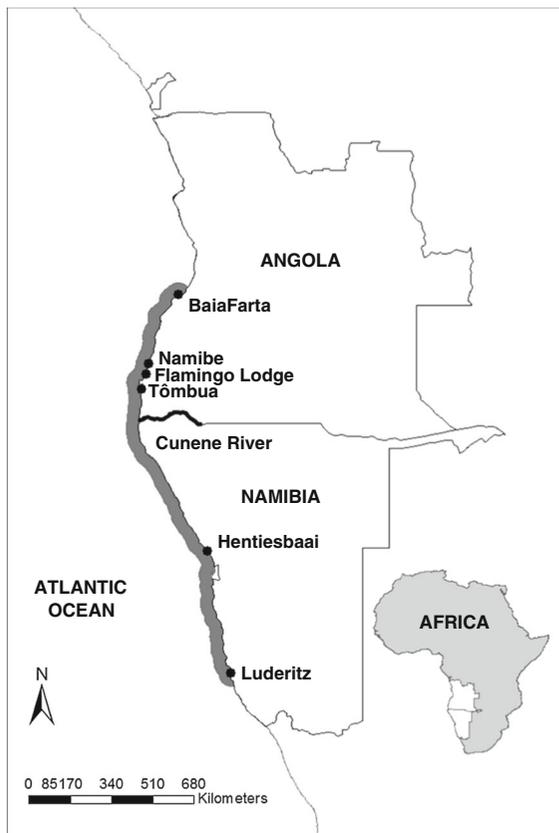


Fig. 1 Map showing the present known distribution of *Diplodus sargus capensis* on the west coast of southern Africa and the locations mentioned in the text

proportion of females that are ripe and SST. The step-model has the form:

$$PR = \begin{cases} a & \text{if } T > d \\ b + cT & \text{otherwise} \end{cases}$$

where PR is the proportion of ripe females, and a, b and c are estimated coefficients with d being a critical temperature. In the model $d = \frac{a-b}{c}$ is not estimated. Parameter estimates were obtained using non-linear least squares while parameter variability was estimated using parametric bootstrapping with a condition that the proportion of ripe females cannot be below zero.

Least-squares linear regression was used to examine the relationship between GSI and both photoperiod and mean monthly SST. Logistic regression was used to examine the statistical relationship between reproductively ripe fish and both photoperiod and mean monthly SST.

Table 1 Staging criteria used to macroscopically assess the gonads of *Diplodus sargus capensis* in southern Angola (validated microscopically in Richardson 2010)

| Stage | Macroscopic description |
|---------|--|
| Resting | Ovaries are light with no oocytes visible to the naked eye. Testes increase in size and appear as flat white bands. No sperm present in tissue |
| Active | Ovaries increase in diameter and oocytes become clearly visible. Ovaries are orange/yellow. Veins and arteries become visible on ovaries. Testes increase in size taking on a triangular shape in cross-section, creamy-beige in colour and sperm present in the tissue when severed and pressure is applied |
| Ripe | Ovaries large in diameter and yellow. Oocytes large and occupy the entire gonad and veins and arteries large and plentiful. Testes large and creamy white in colour, with sperm plentiful if the testes are cut and gently squeezed |
| Spent | Ovaries bloodshot, flaccid and sac-like with few vitellogenic oocytes visible. Testes shrivelled, reduced in size and grey in colour |

Reproductive seasonality in the *Diplodus sargus* “complex”

Available published information on the spawning activity of fishes belonging to the *D. sargus* complex was collated. The months of observed spawning activity and the average monthly SST associated with those months was noted. In cases where average monthly SST was not available in the Mediterranean, the monthly SST climatology for that location was obtained from http://emis.jrc.ec.europa.eu/emis_3_1.php.

Trends in sea surface temperature

Long-term monthly SST data with a pixel resolution of 4 km² were obtained for the present known distribution of *D. s. capensis*, which extends from Lüderitz (26°38′47″S 15°08′58″E) in southern Namibia to Baia Farta (12°36′31″S 13°12′04″E) in northern Angola (Fig. 1), from 1982 to 2007 using the AVHRR Pathfinder 5.2 (Casey et al. 2010) dataset. All georeferenced pixels adjacent to the seaward side of the landmask were extracted for each month and each year.

Trends in reproductive scope

Total annual reproductive scope by area was defined as the total potential reproductive area per year and

was calculated as the sum of all of the georeferenced SST pixels (each pixel represents 4 km²) that fell within the spawning temperature range of the sub-species complex throughout the Angolan and Namibian distribution of the species. The duration of the spawning season, or seasonal reproductive scope, was calculated as the number of months with SST pixels that were within the spawning temperature range and was calculated for localities with significant fisheries that targeted this species—Namibe, Angola (15°11'07"S 12°06'44"E) and Hentiesbaai, Namibia (22°07'16"S 14°16'27"E). Trends in reproductive scope (by area and season) between 1982 and 2008 were investigated using linear regression with year as the independent variable.

Results

Angola in situ water temperatures

An average of 22 SST measurements were recorded per month. The monthly means ranged from 16.5° to 24.7° C and the mean temperature was 20.4° C for the duration of the study period. There was a clear seasonal pattern with water temperature decreasing in May and remaining cold from June to October after which a sharp increase was observed in November (Fig. 2, top panel). An anomalous drop in the mean water temperature was observed during January.

Reproductive seasonality

There was a clear increase in the proportion of ripe mature females during the cold water months from June to October (Fig. 2, middle panel). Female reproductive activity was low during summer, however, a small increase in the proportion of ripe individuals was observed during January and February. This pattern was mirrored by the GSI information (Fig. 2, bottom panel). *D. s. capensis* with ripe running gonads were observed during months with mean SST of between 16 and 20 °C.

The step-model estimated that the proportion of ripe females declined rapidly until 19.33 °C (95 % CI = 19.0–20.0 °C) after which the proportion stabilised at 0.08 (Fig. 3, top panel). The step-model explained 94 % of the variation within the data.. Significant relationships were noted between female

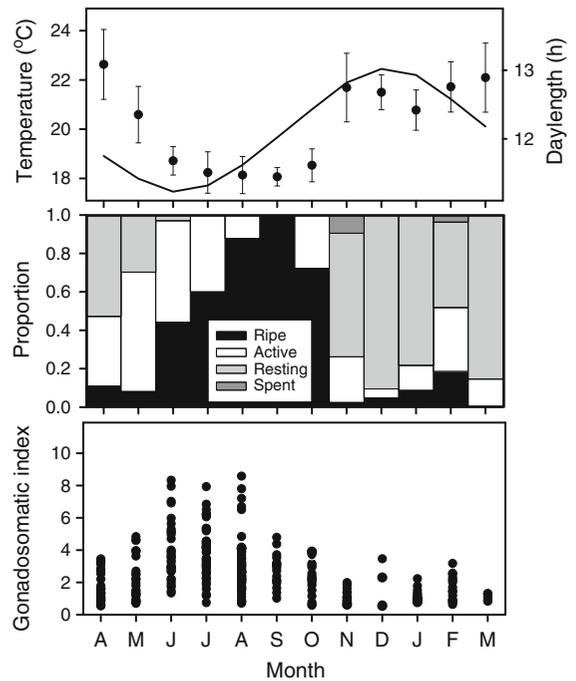


Fig. 2 Mean (\pm SD) surf zone water temperature ($n = 269$) and daylength (*top panel*), percentage of mature fish in different macroscopic stages ($n = 578$) (*middle panel*), and individual gonadosomatic indices ($n = 571$) (*bottom panel*) for mature female *Diplodus sargus capensis* from southern Angola sampled between April 2008 and March 2009

GSI and both photoperiod ($T = -7.12, P < 0.01$) and mean SST ($T = 8.89, P < 0.01$) (Fig. 3, bottom panel). In the case of the monthly proportion of ripe females, only mean SST was found to be statistically significant ($P < 0.01$) (Fig. 3, middle panel). The variance of the data explained by the regression models ranged between $R^2 = 0.26$ and 0.39, respectively.

Metadata analysis

The reproductive biology of the *D. sargus* complex has been studied in the Mediterranean, North Atlantic, South Atlantic, Western Indian Ocean and Persian Gulf (Table 2). A total of 13 studies (including this one) provided information on the spawning periodicity of 14 populations. These populations occurred in areas with monthly average temperatures ranging from 14 to 26 °C. Spawning of *D. sargus* complex occurred between 15 and 20 °C regardless of their location and ambient temperature regime (Table 2).

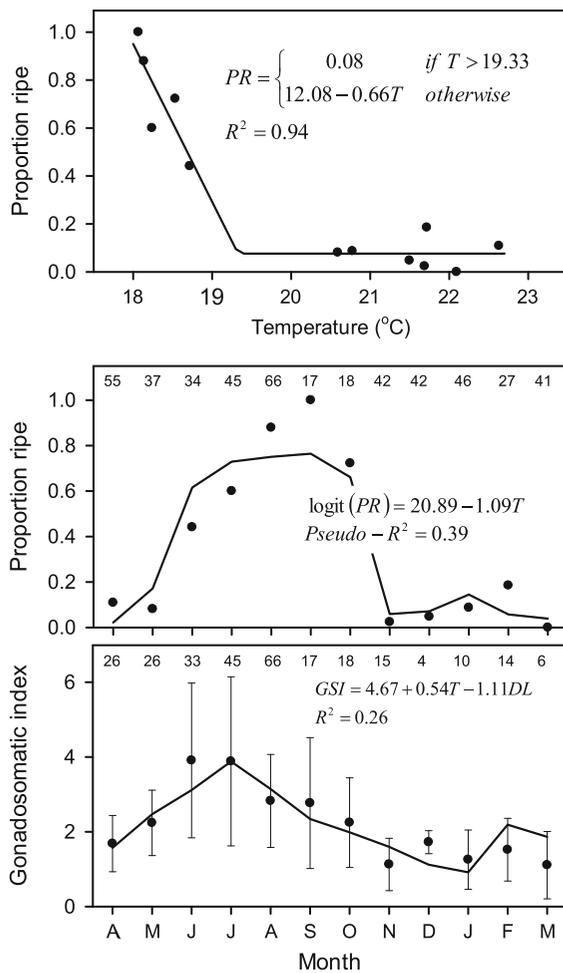


Fig. 3 Observed and predicted proportion of mature female fish with ripe gonads (*top panel*) as a function of mean surf zone water temperature, and the observed and predicted proportion of mature female fish (*middle panel*) and mean (\pm SD) gonadosomatic index (*bottom panel*) for *Dipodus sargus capensis* sampled from southern Angola between April 2008 and March 2009. Sample sizes are included at the top of each panel. *PR* proportion ripe, *GSI* gonadosomatic index, *T* mean surfzone temperature, *DL* day length

Changes in reproductive scope

There was been a general increase in the water temperatures of the northern Benguela region over the last three decades and based on spawning temperatures between 15 and 20 °C, there was a significant ($P < 0.01$) 134 km² (0.7 %) reduction in the annual reproductive scope by area in Angola (Fig. 4, top panel). In contrast, there was a significant ($P < 0.01$) increase of 249 km² (0.6 %), despite possible cyclical trends, in the annual reproductive scope by area in

Namibia (Fig. 4, bottom panel). The reproductive scope of *D. s. capensis* by season, decreased on average by 1.05 months per decade ($P < 0.01$) in the waters of Namibe, Angola compared with an insignificant ($P = 0.08$) increase of 0.76 months per decade in Hentiesbaai, Namibia (Fig. 5). The decreased reproductive scope by season in southern Angola and an increasing trend in northern Namibia is illustrated in Fig. 6 with the Cunene River mouth region (approximately -17° S), the transition zone.

Discussion

Peak reproductive activity for *D. sargus capensis* in Angola coincided with the lowest recorded water temperatures during the study period (June to October) and was found to be significantly correlated with water temperature. The results of the metadata analysis (Table 2) supported these findings, but also showed that regardless of the ambient temperatures, populations in this species complex spawn when the temperatures range between 15° and 20 °C. It appeared that the season (or photoperiod) did not have a major influence on the timing of reproduction in this species. The reasons for the rigid reproductive thermal range are unclear. Being resident, adult *D. sargus capensis* are obviously eurythermic (Table 2) and thus one may expect adults to have a broad reproductive thermal range. However, Sheaves (2006) found that sparids with a tropical distribution reproduce during the coolest period of the year and concluded that it was because of the cool water stenothermy of the early life stages. Generally, gametes, eggs and larvae are more sensitive to environmental fluctuations than adult fishes and have a narrower thermal tolerance (Pörtner and Farrell 2008; Pankhurst and Munday 2011). While there is no specific information on the relationship between larval survival and temperature in the *Diplodus*, Houde's (1989) review of the effects of water temperature on fish larval growth and mortality showed that mortality increased by 0.01 with a 1 °C increase in water temperature. The optimal temperature range for adult spawning activity amongst the *D. sargus* sub-species complex, probably has, like in other fishes (Lobel 1989), been influenced by natural selection through the survival of gametes, eggs and larvae.

The reproductive stenothermy makes the *D. sargus* sub-species complex extremely susceptible to ocean

Table 2 Comparison of the spawning period, duration, temperature and ambient temperatures of *Diplodus sargus* complex throughout the world

| Species | Location, ocean | Spawning period | Spawning duration (months) | Spawning temperature (°C) | Temperature at location (°C) |
|---|--------------------------------------|-----------------|----------------------------|---------------------------|------------------------------|
| <i>D. sargus cadenati</i> ¹ | Canary Islands, Northeast Atlantic | Dec–Apr | 5 | 18–20 | 18–25 |
| <i>D. sargus cadenati</i> ² | Mauritania, Northeast Atlantic | Jan–Apr | 4 | 16–20* | 16–26* |
| <i>D. sargus capensis</i> ³ | Eastern Cape, Southwest Indian | May–Dec | 8 | 16–20* | 16–22* |
| <i>D. sargus capensis</i> ⁴ | KwaZulu-Natal, Southwest Indian | May–Dec | 8 | 17–20* | 17–24* |
| <i>D. sargus capensis</i> ⁵ | Western Cape, Southwest Indian | Aug–Mar | 5 | 17–20* | 16–22* |
| <i>D. sargus capensis</i> ⁶ | Southern Angola, Southeast Atlantic | Jun–Oct | 5 | 16–20 | 16–25 |
| <i>D. sargus sargus</i> ⁷ | Algeria, Western Mediterranean | Feb–Apr | 3 | 15–18* | 15–24* |
| <i>D. sargus sargus</i> ⁸ | Azores, North Atlantic | Mar–Jun | 4 | 15–17 | 14–24 |
| <i>D. sargus sargus</i> ⁸ | Lisbon, Northeast Atlantic | Feb–May | 4 | 16–17* | 15–20* |
| <i>D. sargus sargus</i> ⁹ | Bay of Biscay, Northeast Atlantic | Apr–Jun | 3 | 13–17 | 12–21 |
| <i>D. sargus kotschyi</i> ¹⁰ | Kuwait, Persian Gulf | Nov–Mar | 5 | | |
| <i>D. sargus sargus</i> ¹¹ | Egypt, Eastern Mediterranean | Jan–Apr | 4 | 17–20* | 17–27* |
| <i>D. sargus sargus</i> ¹² | Gulf of Lion, Western Mediterranean | Apr–May | 2 | 14–16* | 14–20* |
| <i>D. sargus sargus</i> ¹³ | Gulf of Tunis, Western Mediterranean | Mar–May | 3 | 15–18 | 14–25 |

*Indicates an estimation based on the sea surface temperature climatology obtained from http://emis.jrc.ec.europa.eu/emis_3_1.php
 1 = Pajuelo and Lorenzo (2004), 2 = Dia et al. (2009), 3 = Lasiak (1981), 4 = Joubert (1981), 5 = Mann and Buxton (1998), 6 = this study, 7 = Bengalel and Kara (2010), 8 = Morato et al. (2003), 9 = Lavín and Cabanas (2000), 10 = Abou-Seedo et al. (1990), 11 = El Maghraby et al. (1982), 12 = Man-Wai (1985), 13 = Mouine et al. (2007)

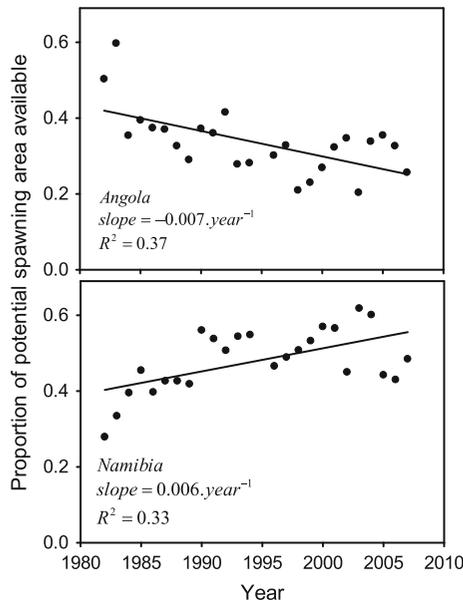


Fig. 4 Total annual reproductive scope of *Diplodus sargus capensis* from Angola and Namibia between 1982 and 2009. Data presented is the area available to spawn per year with temperatures between 15 and 20 °C expressed as a proportion of all area in the study area

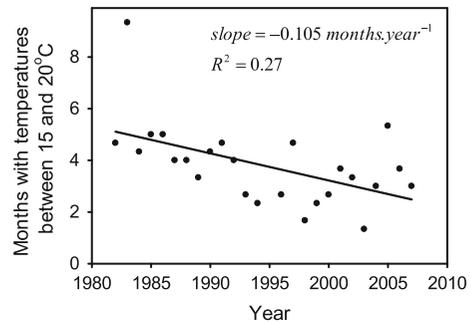


Fig. 5 Seasonal reproductive scope in terms of the duration of the spawning season (months with temperatures between 15 and 20 °C) for *Diplodus sargus capensis* from Namibe, southern Angola between 1982 and 2009

warming, but also allowed the correlative analysis of the trends in reproductive scope. This study showed a decline in the reproductive scope by area of approximately 7 %/decade in Angola. More startling perhaps was the one month per decade reduction in reproductive scope by season in Angola during the study period. As an asynchronous spawning fish that can spawn daily (Mylonas et al. 2011) during favourable

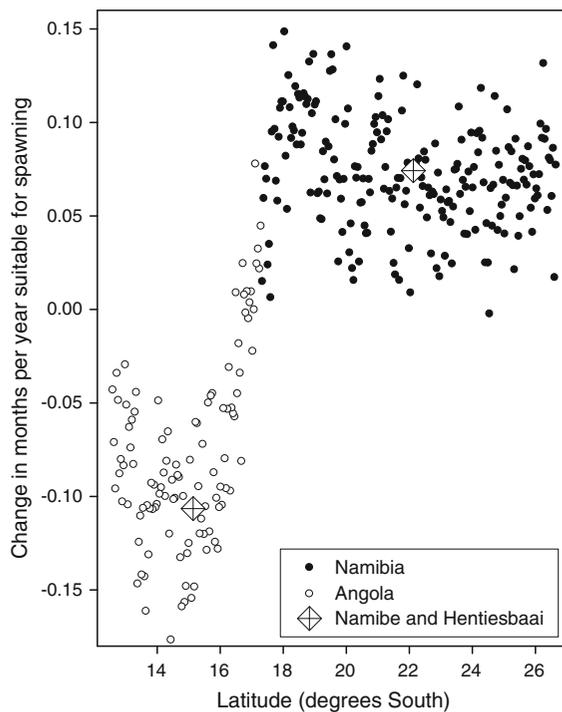


Fig. 6 Annual change in reproductive scope in terms of the duration of the spawning season (months with temperatures between 15 and 20 °C) of *Diplodus sargus capensis* from southern Angola to northern Namibia. Each point represents the slope from a linear regression of months suitable from spawning each year for each pixel (4 km²) against year between 1982 and 2009. The positions of Namibe in southern Angola and Hentiesbaai in northern Namibia are shown and correspond to the results illustrated in Fig. 5

conditions (in this case temperatures between 15 and 20 °C), this equates to a reduction in reproductive output of approximately 20 % per decade.

If this trend was to continue, the reproduction of *D. s. capensis* will cease in Angola within 60 years. Although this may ultimately result in its extirpation in Angola and what we would perceive to be a “distributional shift” of the species, two possible scenarios may prevent this from happening. Firstly, larval connectivity from the Namibian breeding population, which showed a concomitant increase in reproductive scope, may result in the recruitment of juveniles into southern Angola. Although the hydrography of the Mediterranean is not comparable, Di Franco et al. (2012) showed that the pelagic larval dispersal of *D. s. sargus* extended at a scale of between 100 and 200 km. This suggests that at least some recruitment into Angola is possible. However, pelagic larval dispersal

into Angola would require favourable current transport and depend on the availability of suitable temperatures for larval survival. There is very little information on the speed and direction of the coastal currents in northern Namibia. However, Mouton et al. (2001) observed a consistent northward coastal current flow of over 12 cm s⁻¹ during July (which is within the reproductive scope of *D. s. capensis*) in northern Namibia. Although this suggests that the transport mechanism may be available for the eggs and larvae, there is no information to suggest that *D. sargus capensis* eggs and larvae would survive in Angolan waters, when the average water temperatures would exceed 20 °C, if the warming trend continues.

The second scenario that may prevent a local extinction in Angola and a “distribution shift” would be episodic reproductive events during periods with unusually cold water temperatures. As *D. sargus capensis*, like most resident fishes is long-lived, cold temperature anomalies (such as in January during this study) may provide opportunities for reproduction during their lifetime. The maximum age of *D. sargus capensis* in Angola was 20 years and the age at maturity was just under 2 years (Richardson et al. 2011a). Therefore, it is quite conceivable that temperatures favourable for spawning would arise during that 18 year reproductive lifespan of an individual and the population would persist.

The results indicated that the effect of ocean warming was not uniform through the distribution of the species. In contrast to Angola, Namibia was shown to have a 6 % per decade increase in reproductive scope by area, but there appeared to be fluctuations associated with the variable oceanographic conditions in Namibia (Hutchings et al. 2009) within each decade. The primarily southward extension of the reproductive scope by area suggested that reproduction is now possible further south. Therefore, if egg and larval dispersal patterns allow juvenile recruitment, these areas may provide conditions for the southward expansion of the *D. s. capensis* population, ultimately resulting in a distributional shift.

Although changes in reproductive scope may drive distribution shifts in resident species, under the present rates of ocean warming, this mechanism is unlikely to drive the rapid, large-scale distributional shifts predicted for migratory species, where oxygen limitation is the driving mechanism. However, the poleward nature of the shifts predicted for migratory fishes is

also the most likely scenario for resident fishes. Perhaps more importantly, this study has shown that ocean warming may influence the seasonal reproductive scope of resident species and may be a primary mechanism driving variations in the abundance of fishes within their known distribution ranges. Based on these results, it appears that these variations will not be homogenous and ultimately some fisheries may benefit while others will experience declines in fish abundance. For example, in the city of Namibe (Fig. 1) and its close surrounds (4 km north and south of the town), *D. s. capensis* is overexploited (SBR = 20 %, Richardson 2010) and accounts for 82 % of the catch in the subsistence fishery (WMP, unpublished data). With the present one month per decade reduction in the seasonal reproductive scope (Fig. 5, 6), this overexploited population is unlikely to recover even with a reduction in fishing pressure. Therefore, ocean warming is likely to lead to social hardship in this community.

Although the relationship between reproductive output and recruitment success is far from clear (Dixon et al. 1999), an increase in the seasonal reproductive scope of this species in Namibia is expected to lead to improved recruitment success as egg production is considered to be a better indicator of recruitment potential than spawner biomass (Marshall et al. 1998; Sadovy 1996). While there is no significant subsistence fishery for this species, it was the fourth most important teleost species in Namibia (Kirchner et al. 2000) and an increase in recruitment success may ultimately provide improved recreational fishing opportunities and as an important tourist activity, indirect economic gains for the coastal communities of this region.

Sadovy (1996) found that the spawning of reef fishes (excluding sparids) occurred at temperatures below the maximum annual temperatures in many tropical and subtropical regions, such as Kuwait and the Red Sea, Hawaii, the Caribbean, Belau New Caledonia, Fiji and northern Australia. Donelson et al. (2010) found that the reproductive activity of a tropical damselfish (*Acanthochromis polyacanthus*) decreased or ceased in an elevated water temperature regime. Based on these studies, it is likely that other resident fishes would respond in a similar way to the *D. s. capensis* population and one could therefore expect a reduction in the reproductive scope (by area and season) of resident fishes in their tropical distributions, and a concomitant increase in the reproductive scope

of these species in their more temperate distributions. However, in extreme cases, where resident fishes have extremely narrow reproductive temperature range, such as the Nassau grouper (*Epinephelus striatus*) which only spawn at temperatures between 25° and 26 °C (Tucker et al. 1993), the reproductive scope may decrease rapidly, and unless larval distribution allows juveniles of these species to settle in areas with suitable spawning temperatures, extinctions are possible.

One important consideration when predicting the impact of ocean warming on reproductive scope of resident fishes is the adaptability of some species to different thermal regimes (Pankhurst and Munday 2011). Local adaptations to thermal regimes have been observed in the populations of several species (Farrell et al. 2008; Munday et al. 2008). Thermal adaptability is generally considered to be dependent on the genetic variability associated with this characteristic and species with substantial genetic variability should be more adaptable to the affects of rapid warming. To predict the response to ocean warming the adaptability of species of interest should first be evaluated. Since a candidate gene approach would be lengthy and prohibitive, in the interim, a metadata analysis (as conducted in this study), that documents the reproductive thermal range amongst geographically distinct populations is probably the most appropriate method. However, in the absence of published information, laboratory experiments (see Donelson et al. 2010) or a metadata analysis of a closely related species may provide the necessary additional information.

The methods used in this study can be extended to evaluate some of the threats and opportunities facing fisheries that target resident fish species globally. Due to the heterogeneity of the expected changes demonstrated in this study, fisheries managers are likely to face significant challenges, and the requirement to evaluate the impact of changing ocean temperatures on the reproduction of resident fishes in their area. Our results suggest that this may be carried out using a broad range of methods. However, in the absence of an evaluation, some general trends can be expected. A reduction in the abundance or even extirpations can be expected on the equatorial range boundaries of resident fishes. This could be accompanied by a poleward expansion of the populations. On the whole, tropical resident species are expected, to shift into warm-temperate regions. This could, to some degree,

mitigate for the loss of the warm-temperate species, which may move poleward into the cool-temperate zone. Unfortunately, the reductions in the abundance of resident fish in the tropics are unlikely to be mitigated by the “arrival” of any other species and fishing communities in these areas may face hardships in the future. These heterogeneous changes in fish abundance may be accompanied by unexpected changes in the dynamics of fisheries, such as the transboundary shift in the distribution of fishing effort, which may occur due to a perceived “distributional shift” of the target species. Regional Fisheries Management Organisations will have a significant management role in these circumstances and additional fishing effort in certain areas will have to be well monitored and controlled using appropriate catch and/or effort controls.

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