

Dolphin predation pressure on pelagic and demersal fish in the northwestern Mediterranean Sea

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ABSTRACT: Sardine *Sardina pilchardus*, anchovy *Engraulis encrasicolus* and European hake *Merluccius merluccius* represent a significant part of the commercial landings in the Gulf of Lions (northwestern Mediterranean Sea). However, their stocks have shown severe declines during the last decades due to fishing pressure and/or environmental changes. The aim of this study was to estimate the current predation pressure of bottlenose dolphins *Tursiops truncatus* and striped dolphins *Stenella coeruleoalba*—which are abundant in the area—on sardine, anchovy and hake. To do so, we developed an original approach based on several data sets and models (aerial surveys, stomach contents, allometric and stock assessment models) and Monte Carlo simulations to incorporate various sources of uncertainty due to data limitations. Despite the uncertainties, the results showed that dolphin predation pressure on sardine and anchovy was extremely low in the Gulf of Lions (all simulations <0.5% of the available stock), indicating little impact of dolphins on those populations. However, significant predation pressure on hake (median value: 23%) was detected, a value which might have doubled in the last 30 yr because of hake overfishing. Over-exploitation has thus reinforced the natural mortality of hake due to dolphin predation, but this predation pressure remains 2 to 3 times lower than that exerted by fisheries.

KEY WORDS: Predation pressure · Top-down effect · Bottlenose dolphin · Striped dolphin · European hake · Sardine · Anchovy · Gulf of Lions

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INTRODUCTION

Although scientists have often assumed that marine ecosystems are mostly controlled by bottom-up processes (Aebischer et al. 1990, Frederiksen et al. 2006), the reverse effect, i.e. top-down control, or even trophic cascades may nonetheless exist (Ainley et al. 2006, Österblom et al. 2006). Other studies have proposed that control in marine food chains is dynamic and that it can alternate between bottom-up and top-down controls (Litzow & Ciannelli 2007, Cury et al. 2008). In particular, marine mammals play a considerable role within marine ecosystems as their abundances and distributions could impact the struc-

ture and functioning of those ecosystems (Roman et al. 2014, Kiszka et al. 2015). Although they might forage on a large variety of prey, from phytoplankton to fish or other marine mammals (Bowen 1997, Astruc 2005), they are usually considered as top predators and often feed on prey that are also exploited by fisheries (Kaschner et al. 2004, Lockyer 2007). Even where marine mammals are thought to mostly consume non-exploited prey species, local competitions with fisheries could appear as a result of 'regional and temporal aggregations of marine mammals in highly productive areas which are likely to coincide with high density fishing areas' (Kaschner et al. 2004, p. 57). Consequently, interactions between fisheries

and marine mammals and even trophic competition in some cases might occur (Bearzi 2002, Pusineri 2005). These frequent interactions between marine mammals and different types of fisheries have double stakes, as they may induce mortality and serious injury for marine mammals but also serious consequences for fishermen due to depredation within the catch (Bearzi 2002, Werner et al. 2015). In particular, incidental mortality of marine mammals due to by-catch represents an issue for dolphin conservation (Brotons et al. 2008, Read 2008, Reeves et al. 2013). On the other hand, depredation (when dolphins take bait or hooked target fish) is an economic concern both worldwide (Read 2005, Snape et al. 2018) and in the Mediterranean Sea, where it affects mostly immobile fishing gear such as trammel nets and gill-nets (Bearzi 2002, Gnone et al. 2011, Pardalou & Tsikliras 2018) but also longlines (Bearzi 2002), purse seines (Reeves et al. 2001), trawl nets (Reeves et al. 2001) and fish farms (López 2006). Finally, overfishing of dolphin prey species is also known to impact dolphin populations, along with other human activities such as pollution, habitat degradation or loss, tourism and climate change (Coll et al. 2010, Gonzalvo et al. 2014, Pennino et al. 2017).

Most of the fish stocks in the world are either fully exploited (61%) or overexploited (28%) (Sinclair et al. 2002, FAO 2014). This worrying situation is even more acute in the Mediterranean Sea, where an alarming decrease of the main exploited populations has been observed since 1990 (Vasilakopoulos et al. 2014). In those detrimental conditions, the energetic needs for top predators might not always be fulfilled (Bearzi et al. 2006, Österblom et al. 2006, Cury et al. 2011) but also, any additional pressure might affect the stock even more. In particular, natural predation of marine mammals could have additional or synergistic effects on fish stocks. Although the striped dolphin *Stenella coeruleoalba*—the most abundant dolphin in the Mediterranean Sea—feeds mostly on non-commercial prey, it can sometimes also exploit highly valuable commercial resources, such as European hake *Merluccius merluccius* and small pelagics in the western Mediterranean Sea (Bearzi 2002, Gómez-Campos et al. 2011, Aznar et al. 2017). Additionally, the bottlenose dolphin *Tursiops truncatus* mostly resides on the continental shelf during summer (Laran et al. 2017), where most of the Mediterranean fisheries operate, and feeds preferentially on demersal prey such as the European hake, resulting in potentially high interactions with several local fisheries (Bearzi 2002, Kaschner et al. 2004, Gonzalvo et al. 2014).

In the Gulf of Lions, sardines *Sardina pilchardus* and anchovies *Engraulis encrasicolus* have high economic interest, and, until the mid-2000s, their landings represented up to 50% of total annual landings (Bănaru et al. 2013). European hake is also a significant part of the commercial landings in this area and has a high economic value (Mellon-Duval et al. 2017). However, stocks of European hake and small pelagics (both sardines and anchovies) have shown important declines during the last decades (GFCM 2017a,b). The decline in European hake stock is a clear and well-documented case of overfishing due to overcapacity (GFCM 2017a), while environmental changes appear as the main drivers in the decline in condition and size of small pelagic fish in the Gulf of Lions (Van Beveren et al. 2014, Saraux et al. 2018). In those already poor conditions for small pelagics and hake, natural predation of top predators could have more of an impact. The predation pressure of Atlantic bluefin tuna *Thunnus thynnus* on both sardines and anchovies in the Gulf of Lions has recently been studied and shown to be low (<2%; Van Beveren et al. 2017) but no study has focused on marine mammals in this area. Yet marine mammals seem to be important consumers of prey in various ecosystems, especially cetaceans because of their large body sizes and relatively high metabolic rates (Bowen 1997, Laran et al. 2010). While 3 studies reported prey consumption by dolphins in French marine areas (the Bay of Biscay; Pusineri 2005, Spitz et al. 2018 and the Ligurian Sea; Laran et al. 2010), no study has estimated the predation pressure this could exert on the prey (i.e. prey consumption related to the actual amount of prey biomass). The estimation of predation pressure indeed requires a large and diversified amount of information both on prey and predators (Essington et al. 2001), which is difficult to obtain for marine species because of practical constraints in observing animals (Van Beveren et al. 2017). Bottlenose and striped dolphins are the 2 main dolphin species in the Gulf of Lions (Laran et al. 2017). Their diets are principally composed of fish and cephalopods. European hake is the main prey of bottlenose dolphins and also appears in the striped dolphin diet, while small pelagics, especially sardines, are present in the diet of both dolphin species (Astruc 2005, Gómez-Campos et al. 2011).

In this study, we aimed to assess, for the first time, the predation pressure exerted by the 2 dolphin species (bottlenose and striped dolphins) on the main exploited fish (European hake, sardine and anchovy) in the Gulf of Lions. To do so, we used and adapted an original approach previously developed by Van

Beveren et al. (2017), which combines several data sources on prey and predators (aerial surveys, stomach contents or individual energetic values) and modeling approaches (energetic, stock assessment and statistical models). To take into account the numerous data limitations and estimate the uncertainty associated with our estimations, we further developed a simulation framework, similar to the approach recently used by Spitz et al. (2018).

MATERIALS AND METHODS

Gulf of Lions

The Gulf of Lions is located in the northwestern Mediterranean Sea (Fig. 1) with a bathymetry between 0 and 2500 m and covering about 15 000 km² (Mellon-Duval et al. 2017). The dominant forcing drivers in the area are the strong northwestern (tramontane) and northern (mistral) winds, the western Mediterranean mesoscale circulation and the freshwater input from the Rhone River (Millot 1990, Petrenko et al. 2005). The Gulf of Lions represents an important feeding area for fish, birds and mammals, for both resident and migratory populations (Bănaru et al. 2013).

Dolphin predation pressure

To estimate dolphin predation pressure, 5 different processes must be taken into account: 3 regarding the predators (their abundance, diet and energetic

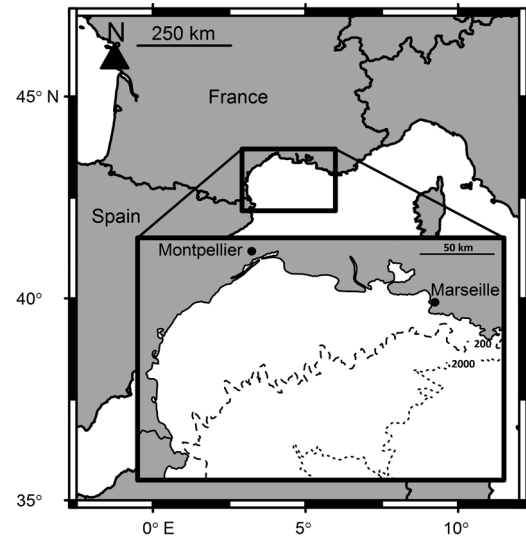


Fig. 1. Gulf of Lions, showing 200 and 2000 m bathymetry

demands) and 2 regarding their prey (their energetic values and stock biomass; Fig. 2). Dolphin predation pressure on a given prey was calculated as follows:

$$\text{Predation pressure} = \frac{\sum_{i=1}^{nb_{\text{dolphin}}} \left(DEE_i \times \frac{\%W_{i,k}}{\sum_{j=1}^{nb_{\text{prey}}} \%W_{i,j} \times E_j} \times \frac{1}{\alpha_i} \right) \times 365}{\text{stock}_k} \quad (1)$$

where nb is the number of dolphins or prey, *i* represents a given dolphin in the population, *E_j* is its daily energy expenditure depending on its mass and

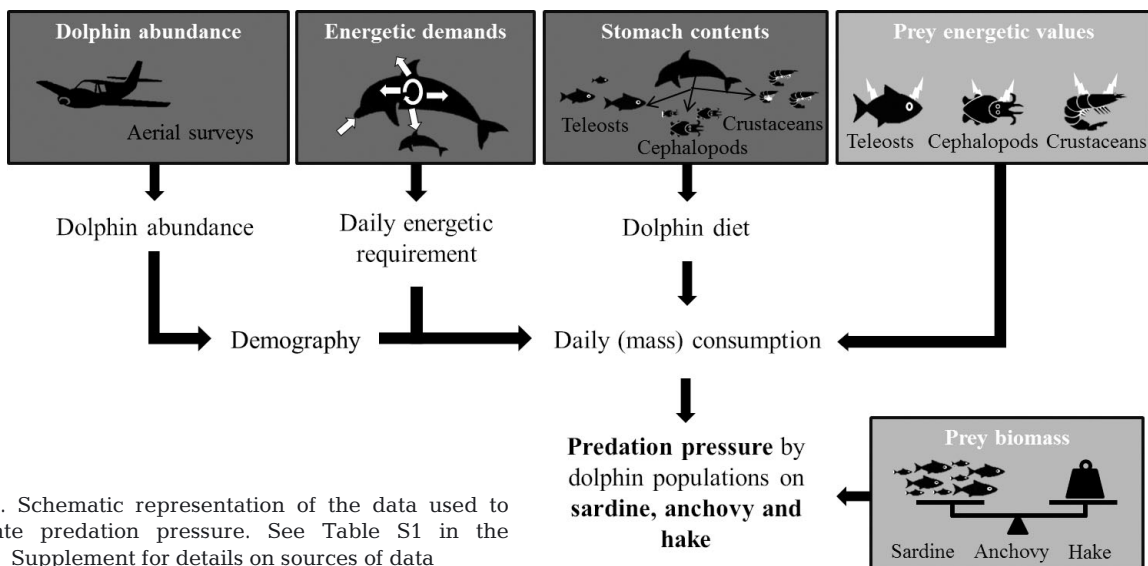


Fig. 2. Schematic representation of the data used to estimate predation pressure. See Table S1 in the Supplement for details on sources of data

reproductive status, $%W_{i,j}$ is the percentage of biomass of prey j in its diet, E_j is the energy content of prey j , α_i is the assimilation efficiency and $stock_k$ is the stock biomass of prey k .

The estimation of predation pressure thus implies several steps, especially to estimate the dolphin population and demography or their daily consumption. As the estimations of the parameters related to these processes of interest exhibit substantial uncertainty (e.g. unknown energetic values for some prey species in the Gulf of Lions) and variability (e.g. interseasonal and interannual variability in dolphin abundances), a simulation framework was developed, similar to the method employed by Spitz et al. (2018), in which prey consumption and energy requirements were estimated using Monte Carlo simulations. In our simulation framework, each simulation was divided into 3 main parts ('Dolphin population and demography', 'Daily consumption' and 'Predation pressure'), corresponding to 12 successive steps presented in details in the next sections (see Fig. 3 and Table S1 in the Supplement at www.int-res.com/articles/suppl/m603p013_supp.pdf). Predation pressure was estimated through 10 000 Monte Carlo simulations (Manly 2006), in which each input parameter was drawn from a given distribution (e.g. normal, uniform and gamma distributions) independently of each other. The predation pressure results are presented as 95% confidence intervals (CI) to remove outliers.

Dolphin population and demography (Part 1)

Annual dolphin abundances in the Gulf of Lions (95% CI) were estimated from Ifremer aerial surveys from 2000–2003 and 2009–2012 using the line transect approach (Bauer et al. 2015). Following Bauer et al. (2015), and taking into account uncertainties and year-to-year variations, dolphin abundances were estimated first using uniform distribution from aerial survey years (for the choice of the year) and then a draw following a log-normal

distribution fitted on density and 95% CI of the chosen year (Fig. 3, Part 1, Step 1). As the aerial surveys did not enable us to discriminate between bottlenose and striped dolphins; see Bauer et al. 2015), we assumed that the dolphin abundance estimated in this study represented the sum of both bottlenose and striped dolphin populations. The striped dolphin is the most abundant species in the northwestern Mediterranean Sea (around 90% of dolphins), with larger group sizes than bottlenose dolphins (Gannier 2005, Gómez De Segura et al. 2008, Laran et al.

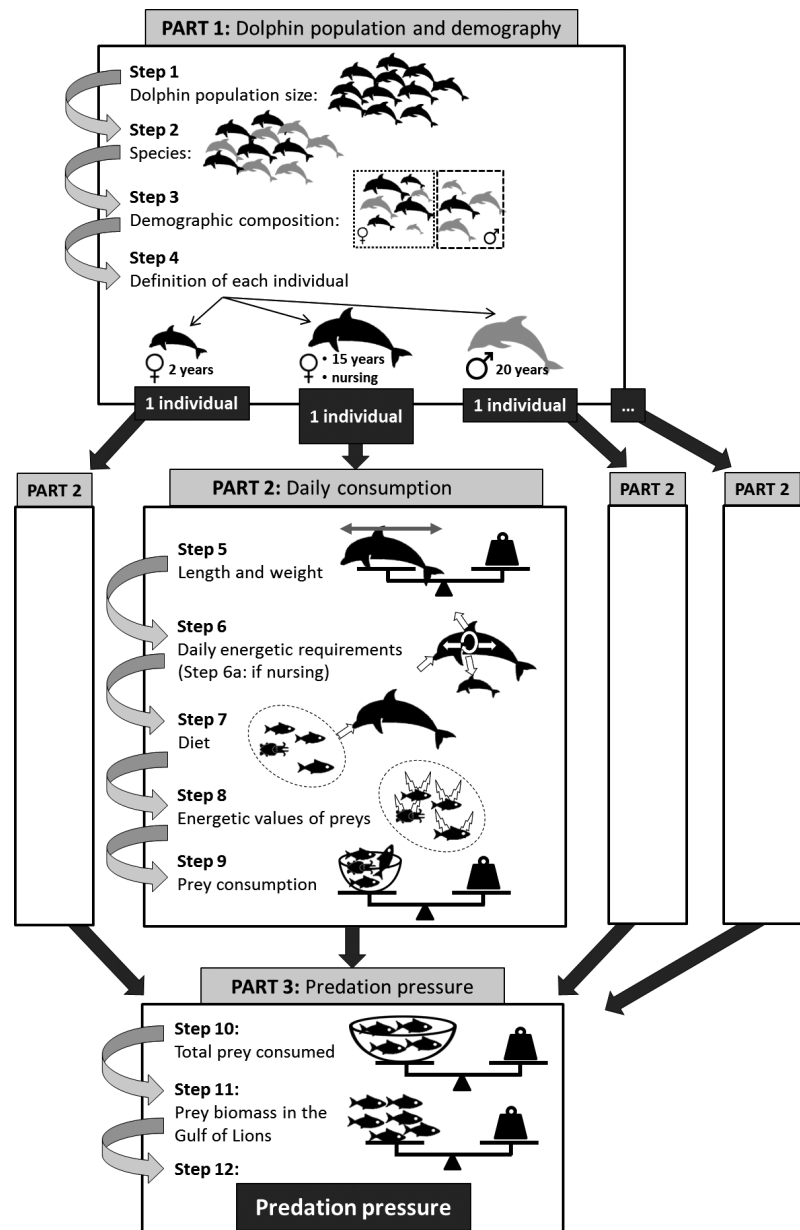


Fig. 3. Schematic representation of the 12 steps (3 parts) of the simulation framework used to estimate predation pressure

2017). However, bottlenose dolphin groups have also been observed in the Gulf of Lions and they could represent a substantial proportion of the dolphin population during summer (Laran et al. 2017, C. Saraux unpubl. data from PELMED surveys). To take this variability into account, a uniform draw was done between 10 and 90% to estimate striped dolphin percentage into the dolphin population for each simulation (Fig. 3, Part 1, Step 2).

Because energy expenditure varies with developmental and reproductive stage as well as body mass (Lockyer 2007), the abundance of dolphins was separated into 3 demographic groups: calves (age 0 to 2; Calzada et al. 1996, Reeves & Read 2003), juveniles (age 2 to 9; Mattson et al. 2006) and adults (age 9 to 35; maximal value observed in Stolen et al. 2002). According to previous studies, dolphin populations are generally composed of 6 to 27% calves, 15 to 30% juveniles and from 43 to 79% mature adults (Wells & Scott 1990, Calzada et al. 1994, Mattson et al. 2006). Sex ratio does not vary much between the 2 species, with 47 to 62% and 43 to 64% of males for bottlenose and striped dolphins, respectively (McFee & Hopkins-Murphy 2002, Stolen et al. 2002, Centro Studi Cetacei 2012). Uniform draws were performed on the above stage-class proportions and sex-ratio values, so that each individual was attributed a sex and stage class (Fig. 3, Part 1, Step 3). Finally, the age of each individual was estimated drawing from a uniform distribution on the age range of its stage class, while a Bernoulli distribution, $B(p)$ (with p equal to the ratio of the number of calves over the number of mature females) was used to assess whether a mature female was nursing. At the end of this first part, each individual of the simulated population was described in terms of species, sex, age and reproductive status (i.e. for mature females whether they were nursing or not) (Fig. 3, Part 1, Step 4).

Daily consumption (Part 2)

Daily energy requirement

Empirical relationships have been commonly employed to quantify requirements of dolphins, baleens or seals, with all of them based on allometry and relationships with body mass (e.g. Sigurjónsson & Víkingsson 1997, Barlow et al. 2008, Laran et al. 2010). Therefore, dolphin age had to be converted into body mass using a combination of age-length and length-mass empirical relationships (summarized in

Tables S2 & S3). Due to a lack of information for striped dolphins, but assuming good correlation between the 2 species, length-mass equations of bottlenose dolphins were used here to estimate mass of striped dolphins (Fig. 3, Part 2, Step 5). The existing length-mass relationships were derived using data from stranding and capture-release projects carried out in the Atlantic Ocean (Table S3); however, data on stranded dolphins in this area are consistent with those relationships (see Fig. S1), although striped dolphins in the Atlantic Ocean appear to be bigger and heavier than those in the Mediterranean Sea (Di-Méglio et al. 1996).

The 3 empirical relationships most frequently used to estimate energy requirements of marine mammals (e.g. Barlow et al. 2008, Laran et al. 2010) were applied to estimate dolphin energy requirements:

$$R = \frac{1}{\alpha} \times \beta \times 293.1 \times M_{\text{dolphin}}^{0.75} \quad (2)$$

(Kleiber 1975),

$$R = \frac{1}{\alpha} \times 690.38 \times M_{\text{dolphin}}^{0.783} \quad (3)$$

(Sigurjónsson & Víkingsson 1997),

$$R = \frac{1}{\alpha} \times 2529 \times M_{\text{dolphin}}^{0.524} \quad (4)$$

(Boyd 2002),

where R is daily energy requirement, α is assimilation efficiency [0.6;0.9], β is the active metabolism factor and M_{dolphin} is dolphin body mass.

Eq. (2) results from an adaptation of Kleiber's equation for basal metabolic rate which has been developed for homeotherms and used on terrestrial mammals (Kleiber 1975, Leaper & Lavigne 2007). This equation assumes that the metabolism of cetaceans is 2 to 3 times (sometimes even 5 times) higher than the basal metabolic rate (Lavigne et al. 1986, Kenney et al. 1997, Pusineri 2005, Rechsteiner et al. 2013). We therefore assumed to draw β from a Gamma distribution, with mean equal to 2.5 and the 99% CI upper value equal to 5 (i.e. shape parameter of 8.33 and scale parameter of 0.30). The assimilation factor, which is usually assumed to vary between 0.7 and 0.8 (Lockyer 1981), could vary with prey condition, size and species (Leaper & Lavigne 2007). To take into account this variability, α was randomly drawn following a uniform distribution between 0.6 and 0.9.

In our simulations, R was estimated using first a uniform draw on the 3 empirical relationships (for the

model choice) and then a uniform and gamma draw on its coefficients (α and β) (Fig. 3, Part 2, Step 6). A sensitivity analysis of energy requirement models was performed reproducing the same framework 3 times, once per equation. Finally, nursing females have additional requirements due to suckling. For that reason, their energetic demand requires an increase estimated to be between 48 and 97% (see Kastelein et al. 2002, 2003). This was taken into account in the simulation using a uniform draw on those additional requirements for nursing females (Fig. 3, Part 2, Step 6a).

Dolphin diet

Dolphin diet was estimated using previously published stomach content data. These data were aggregated, summing abundance, weight and occurrence by prey species (see Tables S4 & S5). Briefly, these data had been acquired from by-catch or stranded dolphins along the Mediterranean coasts. Prey was identified using tough pieces (otoliths and cephalopod beaks) and body length and mass were estimated either directly or indirectly through empirical relationships or by using the mean body mass of the species (see Würtz & Marralle 1993, Astruc 2005). From this data, we calculated $\%W_{i,j}$, the percentage of biomass of prey j (family or species) in the diet of dolphin i .

Aside from the 3 species of interest (i.e. hake, sardine and anchovy), all species contributing to at least 1% of biomass were kept for further analyses.

Prey consumption

Daily prey consumption was estimated using energy requirements and diet (in terms of biomass and energetic values of prey; Fig. 3, from Part 2, Step 7 to 9). To convert prey biomass into energy, energetic values of each prey item had to be known. Instead of assuming a generic energetic value for each prey class (e.g. demersal fish), we used specific values for each of the 27 prey species (see Table S6). When energetic values were not available at the species level (in about half of the cases), we used energetic values available at the lowest phylogenetic level. Further, energetic values can vary between years, seasons and geographic zones (Spitz et al. 2010). To take into account both sources of uncertainties, the energetic value of each prey species was estimated using a normal distribution $N(\mu, \sigma)$ of the

mean (μ), in which the variance (σ) depended on the taxonomic level at which information was available (Fig. 3, Part 2, Step 8, Table S6). Then the total daily consumption as well as the daily biomass of each prey species consumed per day were estimated for each dolphin as follows:

$$C_i = \frac{R_i}{\sum_j (\%W_{i,j} \times E_j)} \quad (5)$$

where C_i (kg d^{-1}) is the total amount of prey ingested daily by dolphin i and R_i is the daily energy requirement of dolphin i . This gives the biomass of prey j consumed per day by dolphin i ($C_{i,j}$) as:

$$C_{i,j} = C_i \times \%W_{i,j} \quad (6)$$

The biomasses of European hakes, sardines and anchovies consumed per day were calculated using Eq. (6) (Fig. 3, Part 2, Step 9). As the diet composition and energy content of the prey were assumed to be constant throughout the year, in the absence of more detailed information on seasonal variations, daily consumptions were summed over all dolphins during 1 yr to estimate annual consumptions (Eq. 1 and Fig. 3, Part 3, Step 10). However, our study integrates temporal changes in these 2 parameters, as the diet and energy content data result from samples collected during all seasons.

Predation pressure (Part 3)

Annual stock biomass of small pelagics was calculated using data collected from scientific acoustic surveys carried out by Ifremer every summer from 1993 to 2016 (PELAGIQUES MEDiterrannée [PELMED]; described in Saraux et al. 2014). European hake biomass in the Gulf of Lions was derived from data collected during annual standardized bottom trawl scientific surveys (MEDITS Working Group 2013) and stock assessment modelling (GFCM 2017a). Here, for each Monte Carlo simulation, stock biomasses of hake, sardine and anchovy were estimated by uniform draw between minimal and maximal values of stock biomasses to take into account year-to-year variations and inherent uncertainties in stock assessment procedures (i.e. sardine: 26 054 to 264 024 t, anchovy: 13 654 to 112 018 t, hake: 2755 to 5348 t; GFCM 2017a,b) (Fig. 3, Part 3, Step 11). The predation pressure on each species was finally estimated as the ratio between its biomass consumed by dolphins and its stock biomass in the Gulf of Lions

(Fig. 3, Part 3, Step 12). All simulations were performed using R (R Core Team 2018).

RESULTS

Dolphin population

According to Bauer et al. (2015), and taking into account year-to-year variations, dolphin densities were estimated to be between 0.031 and 0.345 dolphins km^{-2} (medians of minimal and maximal boundaries of 95% CI). Multiplying these densities by the surface of the study area, populations of dolphins were estimated at between 460 and 5160 individuals in the Gulf of Lions.

Daily consumption

Dolphin daily energy requirements

Mean mass was higher for bottlenose than striped dolphins regardless of the developmental stage (e.g. adult mean \pm SD mass was estimated at 187 ± 17 and 86 ± 4 kg for bottlenose and striped dolphins, respectively; Table 1). Using allometric relationships, the mass of each dolphin was converted into energy requirements. Mean (\pm SD) energetic demands of bottlenose dolphins were about 1.6 times higher than those of striped dolphins for a given stage (e.g. $61\,700 \pm 19\,800$ and $38\,200 \pm 13\,600$ $\text{kJ d}^{-1} \text{ ind.}^{-1}$ for adult bottlenose and striped dolphins, respectively; Table 1). Conversely, mass-specific requirements of bottlenose dolphins were lower than those of striped dolphins, but the difference in energy requirements between stages within the same species was small (between 325 and 335 kJ kg^{-1} and between 422 and 439 kJ kg^{-1} for bottlenose and striped dolphins, respectively; Table 1).

Dolphin diet and energetic values of prey

Diets of both dolphin species were dominated by teleosts in terms of prey abundance (about 89 and 63% for bottlenose and striped dolphin, respectively; Tables S4 & S5). However, the picture is different in terms of biomass. Bottlenose diet was dominated by teleosts (86%; Table S4), while that of the striped dolphin was dominated by cephalopods (66%; Table S5). Besides these 2 dominant groups of prey, crustaceans were also present in dolphin diets but represented less than 5% of the prey in terms of abundance and biomass (Tables S4 & S5).

European hake was the dominant prey for bottlenose dolphins in terms of abundance (32%), biomass (30%), frequency and index of relative importance (IRI) (Fig. 4a, Table S4). Although blue whiting was the most abundant prey in terms of abundance (17%) for the striped dolphin (Fig. 4b, Table S5), squids played a key role in its diet in terms of abundance (32%), biomass (65%) and IRI (56%). The main squid species in terms of biomass were the European flying squid, European squid and reverse jewel squid (Fig. 4b, Table S5). Sardine and anchovy consumptions were low for both dolphin species but sardine could represent up to 5% of the striped dolphin diet in terms of biomass (Fig. 4b, Table S5).

Finally, 27 prey species were kept for the study ($\%W > 1\%$ together with sardine, anchovy and European hake), representing about 94 and 89% of biomass consumed by bottlenose and striped dolphins, respectively (Fig. 4). Energetic values of sardine and anchovy were higher than that of European hake (10.2 ± 2.9 , 7.0 ± 3.0 and 3.9 ± 0.2 kJ g^{-1} respectively; Table S6). In general, fish prey had greater energetic values than cephalopods. All energetic values of prey are summarized in Table S6.

Table 1. Mean (\pm SD) length, mass, individual energetic requirements per day and per kg mass, daily consumption and mass-specific consumption (daily consumption/mass) for all 3 developmental stages of both dolphin species

Species	Stage	Length (cm)	Mass (kg)	Individual daily energetic requirements ($\text{kJ d}^{-1} \text{ ind.}^{-1}$)	Energetic requirements per kg (kJ kg^{-1})	Daily consumption ($\text{kg d}^{-1} \text{ ind.}^{-1}$)	Mass-specific consumption (%)
Bottlenose dolphin	Adults	252 ± 7	187 ± 17	$61\,700 \pm 19\,800$	335 ± 121	11.3 ± 3.7	6.1 ± 2.3
	Juveniles	224 ± 15	133 ± 27	$42\,300 \pm 10\,400$	325 ± 72	7.7 ± 2.0	5.9 ± 1.4
	Calves	167 ± 23	57 ± 21	–	–	–	–
Striped dolphin	Adults	196 ± 3	86 ± 4	$38\,200 \pm 13\,600$	439 ± 152	9.0 ± 3.3	10.3 ± 3.7
	Juveniles	176 ± 13	64 ± 13	$26\,700 \pm 7\,100$	422 ± 106	6.3 ± 1.7	9.9 ± 2.6
	Calves	130 ± 13	26 ± 7	–	–	–	–

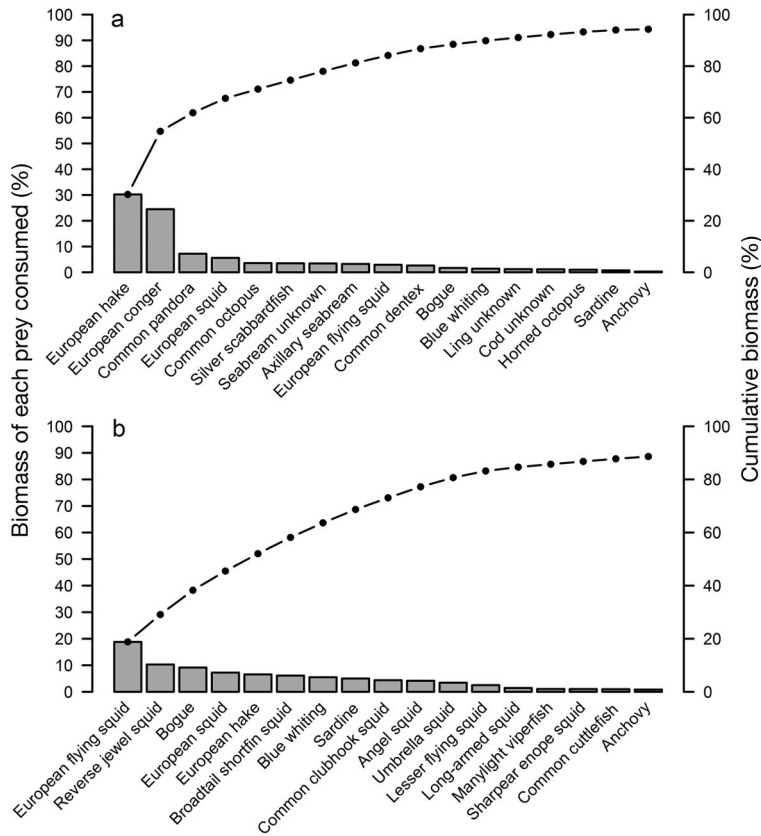


Fig. 4. Percent individual and cumulative biomass of principal prey species consumed by (a) bottlenose and (b) striped dolphins in the northwestern Mediterranean Sea between 1985 and 2012 (see Table 3 for species names)

Dolphin prey consumption

Dolphins consumed $9 \pm 4 \text{ kg d}^{-1} \text{ ind.}^{-1}$ of prey, i.e. $8 \pm 3\%$ of their own mass per day. This consumption was higher for bottlenose dolphins in terms of $\text{kg d}^{-1} \text{ ind.}^{-1}$ (with $11.3 \pm 3.7 \text{ kg d}^{-1} \text{ ind.}^{-1}$) (mean \pm SD, for all subsequent values), but higher in terms of mass-specific consumption for striped dolphins ($10.3 \pm 3.7\%$, Table 1). Assuming constant daily alimentation throughout the year, the total amount of prey ingested by dolphins in the Gulf of Lions was $6400 \pm$

6700 t yr^{-1} , which corresponds to $424 \pm 444 \text{ kg km}^{-2} \text{ yr}^{-1}$.

Among the 3 species of interest, dolphins consumed mostly European hake (about $1250 \pm 1461 \text{ t yr}^{-1}$, and this consumption was mainly due to the bottlenose dolphin ($1065 \pm 1353 \text{ t yr}^{-1}$, i.e. $3.1 \pm 1.1 \text{ kg d}^{-1} \text{ ind.}^{-1}$; Table 2). Annual consumption of both sardine and anchovy was much lower than hake ($203 \pm 222 \text{ t yr}^{-1}$) and mostly by striped dolphins ($166 \pm 198 \text{ t yr}^{-1}$, which mostly consumed sardine ($142 \pm 169 \text{ t yr}^{-1}$; Table 2). Median values and 95% CI of annual consumption of main prey by bottlenose and striped dolphins are summarized in Table 3.

Dolphin predation pressure

To estimate predation pressure of dolphins in the Gulf of Lions and to take into account the variability of intermediate processes, 10 000 dolphin populations were simulated, corresponding to about 16 million individuals. The median predation pressure of both dolphin species on hake was estimated at around 23% (95% CI: 5–110%; Fig. 5a), while predation pressure estimates on sardine and anchovy were always lower than 0.5% (note that the predation pressure on sardines was twice as high as on anchovies: median of 0.09% [95% CI: <0.1 to 0.5%] and 0.05% [95% CI: <0.1 to 0.2%] for sardine and anchovy, respectively; Fig. 5b,c). Testing the sensitivity of these results to the equations used to estimate daily energetic requirements, we found similar results with all 3 equations: predation pressure estimation on hake (considering each energy relationships separately) led to 21, 24 and 24% for Eqs. (2), (3) & (4) respectively while predation pressure differences were <0.1% for small pelagics (Fig. S2).

Table 2. Mean (\pm SD) annual and individual daily consumption of European hake, sardine and anchovy by bottlenose and striped dolphins

Species	Annual hake consumption (t yr ⁻¹)	Individual daily hake consumption (kg d ⁻¹ ind. ⁻¹)	Annual sardine consumption (t yr ⁻¹)	Individual daily sardine consumption (kg d ⁻¹ ind. ⁻¹)	Annual anchovy consumption (t yr ⁻¹)	Individual daily anchovy consumption (kg d ⁻¹ ind. ⁻¹)
Bottlenose dolphin	1065 \pm 1353	3.1 \pm 1.1	26 \pm 33	0.1 (<0.1)	11 \pm 13	<0.1
Striped dolphin	185 \pm 220	0.5 \pm 0.2	142 \pm 169	0.4 \pm 0.2	24 \pm 29	0.1 (<0.1)

Table 3. Median and 95 % CI of annual consumption of main prey (in tons) by bottlenose and striped dolphins

Species	Common name	Bottlenose dolphin		Striped dolphin	
		Median	95 % CI	Median	95 % CI
<i>Merluccius merluccius</i>	European hake	749	112–3693	131	19–649
<i>Conger conger</i>	European conger	607	91–2993	–	–
<i>Pagellus erythrinus</i>	Common pandora	179	27–881	–	–
<i>Loligo vulgaris</i>	European squid	139	21–683	145	21–718
<i>Octopus vulgaris</i>	Common octopus	88	13–436	–	–
<i>Todarodes sagittatus</i>	European flying squid	72	11–357	376	53–1864
<i>Lepidopus caudatus</i>	Silver scabbardfish	87	13–427	–	–
<i>Pagellus sp.</i>	Seabream unknown	85	13–421	–	–
<i>Pagellus acarne</i>	Axillary seabream	80	12–396	–	–
<i>Dentex dentex</i>	Common dentex	65	10–320	–	–
<i>Boops boops</i>	Bogue	42	6–207	183	26–907
<i>Micromesistius poutassou</i>	Blue whiting	34	5–170	110	16–545
<i>Molva sp.</i>	Ling unknown	30	5–149	–	–
Gadidae sp.	Cod unknown	29	4–143	–	–
<i>Eledone cirrhosa</i>	Horned octopus	25	4–123	–	–
<i>Sardina pilchardus</i>	Sardine	18	3–90	100	14–499
<i>Engraulis encrasicolus</i>	Anchovy	7	1–37	17	2–84
<i>Histioteuthis reversa</i>	Reverse jewel squid	–	–	206	29–1021
<i>Illex coindetii</i>	Broadtail shortfin squid	–	–	122	17–606
<i>Onychoteuthis banksii</i>	Common clubhook squid	–	–	88	12–434
<i>Ancistroteuthis lichtensteini</i>	Angel squid	–	–	83	12–413
<i>Histioteuthis bonnellii</i>	Umbrella squid	–	–	69	10–341
<i>Todaropsis eblanae</i>	Lesser flying squid	–	–	50	7–250
<i>Chiroteuthis veranyi</i>	Long-armed squid	–	–	29	4–144
<i>Chauliodus sloanei</i>	Manylight viperfish	–	–	22	3–108
<i>Ancistrocheirus lesueurii</i>	Sharpear enope squid	–	–	21	3–104
<i>Sepia officinalis</i>	Common cuttlefish	–	–	20	3–99

DISCUSSION

Potential sources of variability

This study aimed to estimate the predation pressure of the 2 main dolphin species on commercial fish inhabiting the Gulf of Lions, especially hake, sardine and anchovy. Predation pressure was estimated by combining 5 different processes requiring a large quantity and variety of data on both prey and predators, which probably explains why this work represents, to our knowledge, the first estimation of dolphin predation pressure in the Mediterranean Sea. Nonetheless, some data sources, such as dolphin censuses, displayed high variability, while other data was missing (e.g. prey energetic value at the species level for all species), leading to uncertainties in the predation pressure estimates. To account for such data limitations and quantify the uncertainty around our result, we developed a method based on Monte Carlo simulations in which each parameter was drawn from a given distribution rather than using a mean value.

Sensitivity analyses of similar models have demonstrated that abundance estimates and residency

ratios are the most influential parameters in consumption estimations (Smith et al. 2015, Spitz et al. 2018). In our study, dolphin abundance estimation was a process with relatively high variability and uncertainty. Indeed, dolphin abundance varied between 460 and 5160 individuals according to year-to-year variations estimated by Bauer et al. (2015). However, this did not take into account possible seasonal variations, which are suspected to be important but remain difficult to estimate because of a lack of data. Nonetheless, the range of our estimations is close to past estimates of dolphins in the Gulf of Lions. Based on 2 seasons and 1 given year, Laran et al. (2017) estimated striped dolphin abundance to be between 424 and 8300 individuals in winter (95 % CI) and bottlenose dolphin abundance from 466 to 3805 individuals in summer (95 % CI), while Di-Méglio et al. (2015) estimated bottlenose dolphin abundance over 2 yr as 385 to 1095 individuals (95 % CI). Here, the primary source of uncertainty probably arises from the proportion of bottlenose versus striped dolphins that inhabit the Gulf of Lions, which was therefore drawn uniformly using a large range of values, i.e. from 10 to 90 % according to different sources

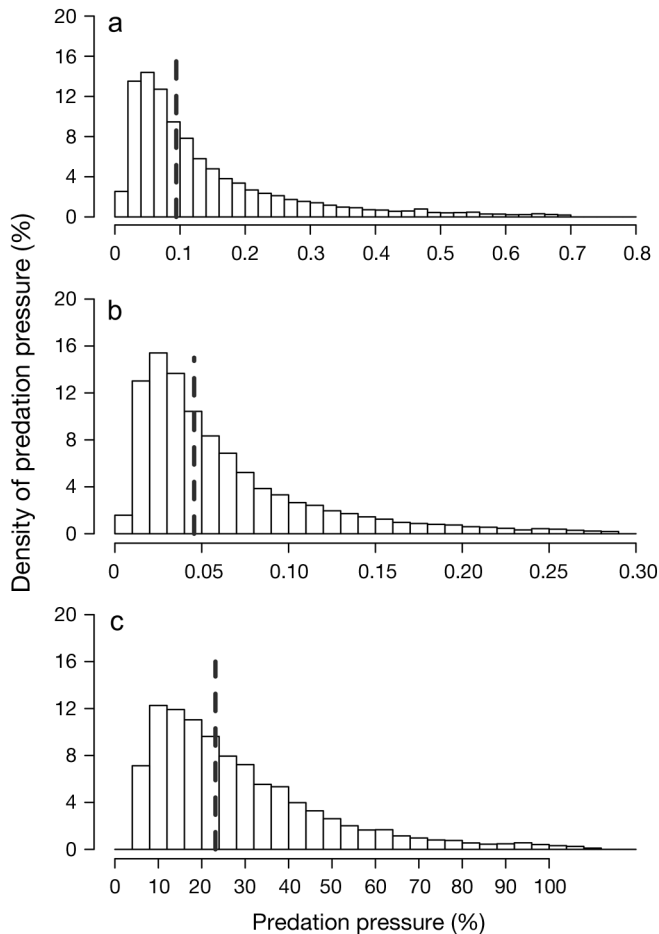


Fig. 5. Dolphin predation pressure (estimated through 10 000 simulations) on (a) sardine, (b) anchovy and (c) European hake. To avoid outliers, 95% CI were plotted. Dashed line = median

(Gannier 2005, Laran et al. 2017, PELMED obs., unpubl. data). As diet differs substantially between the 2 species, this uncertainty propagates into the estimation of hake consumption, which explains the large CI.

After population census, energetic requirements should have the second strongest influence on consumption estimations (Spitz et al. 2018). In our study, we used 3 different energetic models based on the dolphins' body mass, in which a range of values were applied to each model parameter (i.e. assimilation efficiency and active metabolism). Yet the sensitivity analysis on these 3 equations showed that the consequence on the final predation pressure estimate was small for hake (about 1 to 2%) and negligible for both sardine and anchovy (<0.1%), which indicated that the sensitivity of our results did not primarily come from the equations used for dolphin energy require-

ments, but more clearly from dolphin abundance estimations. Additional energetic requirements of nursing females were not negligible (up to 97%; see Kastelein et al. 2002) and were taken into account in our study.

Finally, the seasonal or interannual variability could not always be explicitly estimated in some parameter values or relationships (e.g. in diet or prey energy content). Still, this variability was integrated by using data and results collected from all seasons.

Consumption estimates and energetic requirements

Our median results are of the same order of magnitude as in other studies. Indeed, our estimates of daily consumption of dolphins are close to estimations found for the Ligurian Sea and the eastern Ionian Sea: between 6.3 and 9.0 kg d⁻¹ for the Gulf of Lions (this study), between 2.9 and 6.0 kg d⁻¹ in the Ligurian Sea (Laran et al. 2010) and around 5.4 kg d⁻¹ for the Ionian Sea (Bearzi et al. 2010). Furthermore, annual consumption removal by dolphins estimated here for the Gulf of Lions stands in between estimates of the other 2 Mediterranean areas: 424 ± 444, 999 and 96 kg km⁻² yr⁻¹ for the Gulf of Lions (this study), the Ligurian Sea (Laran et al. 2010) and the Ionian Sea (Bearzi et al. 2010) respectively. Finally, captive adult bottlenose dolphins exhibit similar daily energetic requirements to those found in this study (up to 330 kJ kg⁻¹ of their own mass in captive dolphins at Marineland® of Antibes [M. Oesterwind unpubl. data] compared to 335 ± 121 kJ kg⁻¹ calculated in the present study).

Predation pressure on small pelagics

In the Gulf of Lions, bottlenose and striped dolphins mostly showed little interest in sardine and anchovy, which contributed to <1% biomass of their diet, except for sardines in the striped dolphin diet (5% in terms of biomass). Dolphins are known to display a generalist and opportunistic feeding behavior, as with most top predators, and their feeding regime is also area-dependent. While our results are consistent with previous results from the Bay of Biscay (0 and 3% for striped and bottlenose dolphins respectively; Spitz et al. 2006a,b), sardines have appeared as the key prey for striped dolphins (up to 60%) in some neighboring areas (along the eastern

coast of Spain; Gómez-Campos et al. 2011). The relatively low proportion of sardine (and anchovy) in the dolphin diets from the Gulf of Lions might thus be related to the decrease in biomass, mean length and body condition of those prey in this area (Van Beveren et al. 2014). This has already been observed along the Spanish Mediterranean coasts, for instance, where sardines constituted dolphins' main prey in the 1990s before the proportion of sardines in their diet sharply declined in 2007–2008 as a result of sardine overfishing (Gómez-Campos et al. 2011). These low proportions led to low daily consumption of anchovy ($0.1 \text{ kg d}^{-1} \text{ ind.}^{-1}$ for both dolphin species) and sardine (about $0.3 \text{ kg d}^{-1} \text{ ind.}^{-1}$ for striped dolphins, and lower for bottlenose). Again, these results are similar to those found in the Bay of Biscay, where the consumption of sardine and anchovy was negligible for both dolphin species (up to 0.2 kg of sardines $\text{d}^{-1} \text{ ind.}^{-1}$ for bottlenose dolphins; Pusineri 2005). Consequently, predation pressure on sardine and anchovy was always very low, i.e. below 0.5% in all simulations (median: 0.09% for sardine and 0.05% for anchovy). Predation pressure of dolphins on both small pelagic species is even lower than that of Atlantic bluefin tuna (0.6 ± 0.2 and $1.9 \pm 0.5\%$ for sardines and anchovies respectively; Van Beveren et al. 2017). This predation pressure by dolphins remains significantly lower than the fishing pressure that is estimated (in terms of harvest rate) to be at around 1 and 5% for sardine and anchovy over the last 3 yr respectively (GFCM 2017b). In conclusion, the poor stock status of both sardines and anchovy in the Gulf of Lions (mostly reflected by poor condition and lower growth; see Van Beveren et al. 2014) is unlikely to be due to top-down control by either of the 2 dolphin species. Such a conclusion might also result from the recent absence of common dolphin *Delphinus delphis* in the Gulf of Lions, especially because sardine and anchovy are indeed the main prey of this species regardless of the area considered (Young & Cockcroft 1994, Meynier et al. 2008, Begoña Santos et al. 2014). While the common dolphin might have been expected in the Gulf of Lions due to its preferred habitat (ranging between that of striped dolphin [oceanic habitat] and bottlenose dolphin [coastal habitat]), recent observations are very scarce in the Gulf of Lions, although it seems to have been more common until the middle of the 20th century (Bearzi et al. 2003, Gannier 2017). Reasons for the disappearance of large common dolphin populations in the northwestern Mediterranean basin are still unclear, but may include decrease of

prey availability (e.g. due to competition with local fisheries and/or overfishing), bycatch or hunting before their protection by law, environmental changes (e.g. increase of sea water temperature) or contamination by xenobiotics (Bearzi et al. 2003, Gannier 2017).

Predation pressure on hake

In contrast to small pelagics, consumption of hake by dolphins was significant in the Gulf of Lions, mostly due to bottlenose dolphins. This has been documented in other areas, such as the North Atlantic where it was even higher ($3 \text{ kg d}^{-1} \text{ dolphin}^{-1}$ in the Gulf of Lions vs. 6 and $8 \text{ kg d}^{-1} \text{ dolphin}^{-1}$ off the Iberian Atlantic coasts and in the Bay of Biscay, respectively; Pusineri 2005, Begoña Santos et al. 2014). Nonetheless, the predation pressure of the bottlenose dolphin on European hake was substantial in the Gulf of Lions, but highly variable among the simulations, ranging from 5 to 110% (95% CI), with a median value at around 23%. This large variability probably originates from uncertainties in dolphin abundance census and proportion of the 2 dolphin species (see above). Predation pressure by dolphins on hake remained, however, lower than fishing pressure, which ranged between 38 and 73% over the last 20 yr (from 1998 to 2017; GFCM 2017a). Similar to the fisheries, bottlenose dolphins mainly target ages 0, 1 and 2 of hakes (93% in abundance; see Astruc 2005), so that fishing pressure and dolphin predation act synergistically on juvenile hakes in the Gulf of Lions, potentially amplifying growth overfishing. Our study brings new, objective (quantified from scientific data) information about marine mammal and fisheries interactions in the Northwestern Mediterranean Sea. These interactions usually occur because of competition for a similar resource, and has become a worldwide concern (Morissette et al. 2012, Snape et al. 2018) — both in terms of conservation, as they result in dolphin mortality due to by-catch (Hall et al. 2000, Bearzi 2002) and in terms of economic losses due to depredation or damage to fishing gear (Bearzi 2002, Hamer et al. 2012), even if they could be overvalued in some cases (Trites et al. 1997, Coll et al. 2007, Gazo et al. 2008). This is true in several parts of the Mediterranean Sea (e.g. Lauriano et al. 2009, Gonzalvo et al. 2014) where interactions with fisheries are increasing (Brottons et al. 2008, Pardalou & Tsikliras 2018). Furthermore, overfishing of hake in the Gulf of Lions has generated a strong decline of this population (see GFCM 2017a), which in turn has

reinforced the natural mortality of hake due to dolphin predation. Indeed, predation pressure of dolphins depends on prey population size. Therefore, it is expected to have been lower in the past, as the hake population was significantly larger. The first hake stock assessments in the Gulf of Lions between 1988 and 1991 (stock already overexploited) estimated hake stock biomass to be between 6041 and 9017 t (Aldebert & Recasens 1996). Based on the same simulation framework and assuming the same dolphin population size and demography, the median predation pressure would indeed decrease to about 12% (95% CI: 3 to 57%). This study shows that the predation pressure of dolphins on hake is substantial in the Gulf of Lions and has been further reinforced by current overexploitation of hake. This might have an important impact, especially on bottlenose dolphin populations in coastal waters (Bearzi et al. 2009, Gonzalvo et al. 2014). Therefore, these interactions should be more carefully considered in the future management plans of the European hake stock in the Gulf of Lions for both the conservation of dolphins and the sustainability of the fisheries.

In conclusion, we used an original approach developed by Van Beveren et al. (2017), but went one step further to account for multiple sources of uncertainties in the estimation of predation pressure. We showed that predation pressure of dolphins on sardine and anchovy in the Gulf of Lions was extremely low, indicating that dolphins probably have had little impact on the population dynamics of those exploited fish. In contrast, the predation pressure of dolphins on hake is substantial in the Gulf of Lions and has been further reinforced by current overexploitation of this population. This situation is even more problematic as both the fishing industry and the dolphins prey on the same resource: hake juveniles; a result that should be considered in future management plans of hake populations.

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