



Dynamics of killer whale, bluefin tuna and human fisheries in the Strait of Gibraltar



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ABSTRACT

A complex balance has arisen between the bluefin tuna, killer whales, and human activities in the Strait of Gibraltar. Recent changes in fishing effort have dramatically decreased tuna stocks, breaking this balance. Killer whales exhibit two strategies for feeding on tuna: active hunting and depredation on a drop-line fishery. From 1999 to 2011, a small community of 39 individuals was observed in the Strait in spring and summer. All individuals displayed active hunting and 18 of them also depredated on the fishery. These differences in foraging behaviour influenced life-history parameters. Adult survival for interacting and non-interacting individuals was estimated at 0.991 (SE = 0.011) and 0.901 (SE = 0.050), respectively. Juvenile survival could only be estimated for interacting individuals as 0.966 (SE = 0.024), because only one juvenile and one calf were observed among non-interacting individuals. None of the interacting calves survived after 2005, following the decrease in drop-line fishery catches. Calving rate was estimated at 0.22 (SE = 0.02) for interacting individuals and 0.02 (SE = 0.01) for non-interacting. Calving interval, which could only be calculated for interacting groups, was 7 years. The population growth rate was positive at 4% for interacting individuals, and no growth was observed for non-interacting individuals. These differences in demographic parameters could be explained by access to larger tuna through depredation. Consequently, we found that whales would need more tuna to cover their daily energy requirements while actively hunting. Therefore, our findings suggest an effect of artificial food provisioning on their survival and reproductive output. Urgent actions are needed to ensure the conservation of this, already small, community of killer whales. These include its declaration as Endangered, the implementation of a conservation plan, the creation of a seasonal management area where activities producing underwater noise (i.e. military exercise, seismic surveys or even whale watching activities) are forbidden from March to August, and the promotion of bluefin tuna conservation. Additionally, energetic requirements of this whale community should be taken into account when undertaking ecosystem-based fishery management for the Atlantic bluefin tuna stock. In the meantime, as marine predators are most sensitive to changes in fish abundance when prey abundance is low, we suggest an urgent short-term action. Artisanal fisheries, such as drop-lines, should be promoted instead of purse seiners in the Mediterranean Sea. This will help to maintain the survival and reproductive output of the whale community until showing clear signs of recovery and stability, and/or their prey stock recovers.

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1. Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) (hereafter tuna) perform a gametic migration, entering the Mediterranean Sea through the Strait of Gibraltar (hereafter Strait) in late spring (Sella, 1928, 1929; Rodríguez-Roda, 1964). After spawning, tuna perform a trophic migration to the eastern North Atlantic in summer (de la Serna et al., 2004; Aranda et al., 2013). In the Strait, tuna have been caught for centuries using trap-nets, an artisanal fixed and passive gear (Doumenge, 1998).

In 1995, a new artisanal drop-line fishery was developed by Spain and Morocco in the Strait, to catch tuna on their trophic migration (Srouf, 1994; de la Serna et al., 2004). The Eastern tuna stock has been exploited by traditional fisheries for centuries, but in the 1960s industrial purse-seine and long-line fleets replaced the traditional fisheries (Fromentin and Powers, 2005). Thus, tuna stock has been mostly declining since then (ICCAT, 2011; Taylor et al., 2011).

Other natural predators feed on tuna such as large pelagic sharks and killer whales (*Orcinus orca*) (Fromentin and Powers, 2005). Killer whales have been observed in the Strait for centuries (Horozco, 1598; Richard, 1936; Aloncle, 1964). Stable isotope analyses suggest that their main prey is tuna (García-Tiscar, 2009). They have been assigned

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to a single population in conjunction with whales sampled in the Canary Islands based on nuclear DNA loci (Foote et al., 2011), and thus we define killer whales in the Strait as a community of whales. They occur in the Gulf of Cadiz in spring (Esteban et al., 2013), while they actively forage on tuna around the trap nets using the endurance-exhaustion hunting technique (hereafter active hunting) (Guinet et al., 2007), which consists of chasing tuna at high speed for around 30 min. According to the authors, this technique requires a high energy investment and the average catch is usually small-medium size. It was also suggested that killer whales likely rely on other techniques to catch larger individuals. During summer, the whales are also observed actively hunting in the central waters of the Strait (de Stephanis et al., 2008). However, a new operational and biological interaction has been described between killer whales and tuna drop-line fisheries, where killer whales depredate tuna from their baited hooks, for which they presumably invest less energy (Guinet et al., 2007; de Stephanis et al., 2008; Esteban et al., 2013). Esteban et al. (2015) described five pods in the Strait (A1, A2, B, C and D). While all pods have been seen actively hunting tuna, only two pods (A1 and A2) have learned to interact with the fishery.

The inclusion of artificial food provisioning and a presumably highly energetic resource, such as tuna from fisheries, may influence demographic parameters and reproductive output within these killer whales. Our aims were to elucidate the consequences of this interaction on life-history parameters for interacting and non-interacting killer whales, and compare their energy requirements for interacting or active hunting.

2. Materials and methods

2.1. Data collection

The study area is located between 5 to 6°W. It was surveyed between 1999 and 2011 for cetaceans. More details regarding the sampling protocols can be found in de Stephanis et al. (2008) and Esteban et al. (in press).

2.2. Life history parameters

Photo-identification techniques (e.g. Bigg et al., 1990; Ottensmeyer and Whitehead, 2003) were used as previously described (Esteban et al., 2015) to identify every individual observed in the study area. The photo-identification catalogue is available at www.cetidmed.com, where it is updated annually.

2.2.1. Abundance

Censuses were conducted annually from which a cumulative abundance count was calculated as the total number of individuals observed every year minus those determined to be dead. Killer whales' social structure in the Strait has been suggested to be a matrilineal social structure without individual dispersal from their natal group (Esteban et al., 2015); therefore, an individual was considered dead whenever it was not seen within its pod for three consecutive years or it was found stranded. We used photographs combined with direct observations to determine sex and approximate age of whales (Olesiuk et al., 1990). Following the definition of sexual maturity described in Olesiuk et al. (1990), we sorted the whales into three categories. Adults included males that were mature individuals presenting a prominent dorsal fin and females that were mature individuals accompanied by calves or juveniles; juveniles were individuals older than 1 year but still not mature and calves were individuals younger than 1 year. We also classified whales by their foraging behaviour as either interacting (hereafter INT) for whales observed depredating on the tuna drop-line fishery at least once, or non-interacting (hereafter NOT) for whales that were never observed depredating.

2.2.2. Mark-recapture analysis

As only some pods were seen every year (Appendix A, Table A.1), we used mark-recapture analyses to estimate (1) survival rate for the three

age classes (calf, juvenile, adult) and (2) population growth rate using the software MARK 7.1 (White and Burnham, 1999). All models were compared using QAIC_c (Quasi Akaike's information criterion adjusted for small sample bias) (Sugiura, 1978). The best model was selected by the lowest QAIC_c. Models within $\Delta\text{QAIC}_c \leq 2$ were considered to be well supported by the data (Burnham and Anderson, 2004). In case that $\Delta\text{QAIC}_c \leq 2$, model averaging was used (Buckland et al., 1997).

2.2.2.1. Survival rate. Multistate mark-recapture models (Hestbeck et al., 1991; Brownie et al., 1993) were used to examine differences in survival (S), the probability of an animal to be re-encountered (p) and state transition probabilities (ψ), among the two groups INT and NOT, contained in three different states: adult (A), juvenile (J) and calf (C). To assess the goodness-of-fit of the model, we used a parametric bootstrap procedure implemented in MARK 7.1 (White and Burnham, 1999). The variance inflation factor measuring possible over-dispersion in the data, \hat{c} , was estimated as the deviance estimate from the original data divided by the mean of the simulated bootstrapped deviances and applied to all models if > 1 (White, 2002). For both groups, we constrained state transitions ψ from A to C, A to J and J to C as 0 as these transitions are impossible. We also fixed transitions from C to J as 1, as calves become juveniles after one year of life by our definition. We fixed S_{CNOT} and S_{JNOT} to 1 because the only calf and juvenile in the NOT group were observed the in last year their pod was seen, so survival could not be estimated (Appendix A, Table A.1). For NOT, we fixed $p = 0$ for all age classes in 1999–2001 and 2008–2009 as no animals were seen during these years.

We considered various models to test for differences and similarities of survival between INT and NOT, and through time. We started with the full time-dependent model (t) (Appendix A, Table A.2, model 5). We then fitted a more parsimonious model by constraining all parameters to be constant in time (\cdot) (Appendix A, Table A.2, model 3). To investigate calf survival for INT, we tested it as constant over the study period (model 3), time-dependent (model 4) and fixed to 1 in 1999–2005 and to 0 in 2006–2010, following our direct observation of no calf surviving their first year of life after 2005 (model 1). Finally, we tested for similarities or differences of adult survival between INT and NOT (models 1 and 2).

2.2.2.2. Population growth rate. The population growth rate was modelled with a Pradel model with survival (ϕ) and lambda (λ) (Pradel, 1996). Lambda was modelled as constant in time, and was tested as equal or different for INT and NOT individuals. For NOT, we fixed $p = 0$ in 1999–2001 and 2008–2009 as no animals were seen during these years.

2.2.3. Reproductive rates

Calving rates for INT and NOT were calculated as the total number of calves born during a given year out of the total number of reproductive females available that year within the group. Females calving a year before were omitted for that year, because of their 12 month lactation period (Olesiuk et al., 2005; Kuningas et al., 2013). Females were assigned as reproductive females whenever they were known to be in their reproductive years (10–46 years old) (Olesiuk et al., 2005) or the years they were seen with a calf. A Mann-Whitney-Wilcoxon test was performed to compare annual calving rates between INT and NOT.

Calving interval was calculated as the interval at which the same female gives birth to successive viable calves (Olesiuk et al., 1990) (Appendix A, Table A.3). Fecundity rate was calculated as the reciprocal of calving interval (Olesiuk et al., 1990).

2.3. Interaction between tuna drop-line fisheries and killer whales

Available data on tuna catches by drop-line fisheries in the Strait were compiled from data of the regional Government of Andalusia (Spain) and data from Malouli Idrissi et al. (2013) for Morocco.

No calves survived after 2005. At the same time, tuna has clearly declined in recent decades, and a restrictive quota was settled for drop-line fisheries in 2008 (ICCAT, 2011). We assessed the relationship between SC_{INT} and tuna drop-line catches. We used a Firth's logistic regression to cope with a possible separation problem (Albert and Anderson, 1984), as none or all calves survived in a given year. Firth's penalized log-likelihood (Firth, 1993) was used with the 'logistf' package (Heinze et al., 2013) in the programme R version 3.2.1 (R Development Team Core, 2010). Three possible lagged effects were tested in Spanish and Moroccan catches combined. First, a direct effect on SC_{INT} of catches in the same year (lag0), then a 1-year time lag (lag1), and 2-year time lag (lag2), which may also be appropriate to assess the influence of the amount of depredated tuna on SC_{INT} because of the 18-month gestation period of killer whales (Ford et al., 2005). The model with the lower AIC_c value (Akaike, 1974) was selected and non-significant terms ($p > 0.05$) were excluded. Models within $\Delta AIC_c \leq 2$ were considered to be well supported by the data (Burnham and Anderson, 2004). We also estimated catches of tuna that allow a SC_{INT} at a level similar to populations considered to be of good conservation status. We used as a reference the well-studied population of northern resident killer whales (NRKW) in the North Pacific, which had a calf survival rate of 0.91 in 1996–2004 during a stable period (Olesiuk et al., 2005), and 0.97 between 1973 and 1996 during a period of unrestrained growth (Olesiuk et al., 1990).

Interviews with fishermen were conducted in Tarifa (Spain) in July–August 2004 to estimate the level of interactions with killer whales. Short face-to-face closed-question surveys (3–4 min) were conducted at the landing site (e.g. Huntington, 2000; Renner and Bell, 2008; Fowler, 2013). These daily interviews included questions about the number of tuna caught, killer whale presence and the number of tuna lost due to operational causes or killer whale depredation, with tuna being completely or partially lost (i.e. bitten). We also accounted for the weight and length of tuna sold at the fish market. For tuna bitten by killer whales, we calculated the expected total weight from their length using a tuna weight–length relationship (Anon., 1984). We then estimated the amount of tuna weight lost by subtracting their actual weight after being bitten.

2.4. Energetic requirements of killer whales

We applied gross energy requirement models described by Williams et al. (2011):

$$\ln(E) = \ln(a) + b \cdot \ln(L)$$

where E is energy consumed per day in kcal and L is the length of the whale in cm, and a and b are parameters modelled from 29 captive killer whales captured in Iceland (Williams et al., 2011). We estimated the length of individuals for two groups of whales. First, we estimated the length at age for INT in 2004 using demographic data (age, sex, reproductive status). Secondly, we estimated average length for all individuals (INT and NOT) in 2011. Because NOT individuals are not seen every year, we could not properly estimate their age (Olesiuk et al., 1990). Hence, we used an average length for adult females and males extrapolated from individuals stranded or captured in the nearby area, while juveniles were assigned a medium length of 4 m. Next, we estimated daily and yearly energy requirements for both groups.

Assuming that killer whales in the Strait are mainly feeding on tuna (García-Tiscar, 2009), we converted these energy requirements to the number of fish and tons needed to support killer whales in the Strait for two ways. We did this first yearly assuming that killer whales met their energetic requirements exclusively through active hunting (100% scenario) for both groups; and then seasonally in July and August (Summer scenario) only for the INT group assuming that they met their energetic requirements exclusively through depredation on the drop-line fishery. The energy content of prey items was estimated

assuming that the average caloric value of tuna established by FAO (1989) considered that 58% of tuna weight is edible. Of this, 23.7% is protein at 4.27 kcal/g and 4.6% fat at 4.11 kcal/g. Because we used gross energy requirements (Williams et al., 2011), we also assumed a reasonably equivalent transformation from gross to net energy in wild and captive killer whales of 84.7% (Kriete, 1994; Williams et al., 2004; Williams et al., 2011). For tuna caught through depredation on the fishery, we used the average weight of tuna observed in the fish market in 2004. However, when these whales are actively hunting, they are able to capture tuna ranging between 0.8 and 1.5 m (Guinet et al., 2007), and hence we converted length to weight (Anon., 1984).

2.5. Statement on animal subjects

The study was conducted on wild, free-ranging killer whales. A special permit was obtained from the Spanish Ministry of Environment to approach the whales and enter the restricted area established by law (R.D. 1727/2007). If whales displayed boat avoidance behaviour, encounters were ended.

3. Results

3.1. Data collection

We carried out 21,307 km of effort between 1999 and 2011, including 109 sightings of killer whales. On 91 occasions, INT individuals were observed and NOT individuals were seen 18 times (Appendix A, Figure A.1).

3.2. Life history parameters

3.2.1. Abundance

A total of 20,617 photographs were taken. Photographic effort varied and mainly increased (Fig. 1), due to increasing camera quality and experience. Despite this increased effort, the cumulative curve of individuals identified seems stable over the last several years (Fig. 1). Forty-seven individuals were identified and included in the catalogue. Of these, 2 juveniles, 5 calves (belonging to INT) and 1 adult (stranded animal, belonging to NOT) were considered dead over the study period; therefore, only 39 individuals remained alive in 2011, of which 18 were defined as INT, and 21 as NOT. From 1999 to 2005, additions of new individuals were due to the identification of new pods and births (Fig. 1, see Esteban et al., 2015). Since 2005, all new individuals identified were calves from known females of existing pods (Fig. 1). Consequently, we estimated the first cumulative total abundance count for all whales

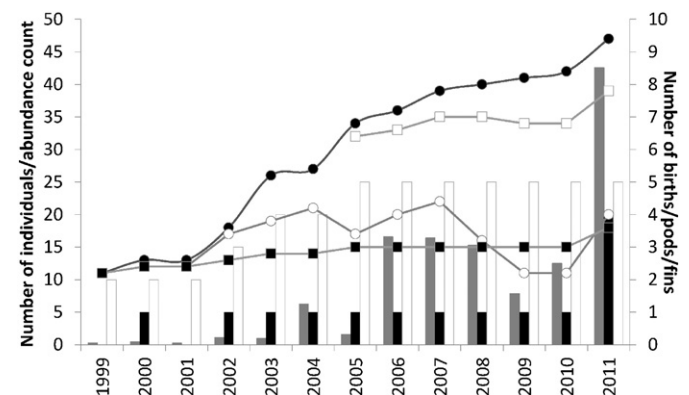


Fig. 1. Summary of killer whales identified between 1999 and 2011. Left axis: black circles indicate cumulative number of individuals identified, white squares cumulative total abundance count and black squares cumulative INT pod abundance count. Right axis: grey bars indicated number of fins analysed in thousand, black bars number of births and white bars cumulative number of pods identified.

in 2005 with 32 individuals, with this number remaining fairly constant until 2011 when 4 births increased the abundance to 39 individuals (Fig. 1). As INT individuals have been seen every year from the beginning of the study, their cumulative abundance count was calculated. In 1999 we counted 11 individuals, between 1999 and 2005 these pods gave birth to 5 viable calves, but 1 juvenile died, increasing the number to 15 individuals in 2005. It then remained fairly constant until 2011, when 3 births increased the number to 18 INT individuals.

3.2.2. Survival rate

Bootstrapped GOF testing allowed the estimation of \hat{c} -hat = 1.63, which indicates a reasonably good model fit to the data (Choquet et al., 2009-pp. 84–75). This value was applied to all models. The best fit model took into account a constant p for all foraging groups and age classes, SC_{INT} fixed to 1 in 99–05 and to 0 in 06–10, a constant S_{INT} , and a constant different SA for INT and NOT (Model 1). The Likelihood Ratio test between models 1 and 2 was highly significant ($\chi^2 = 7.997$, $df = 1$, $p < 0.005$), confirming differences in SA between INT and NOT groups. SA_{INT} was estimated as 0.991 (SE: 0.014; 95% CI: 0.837–1.000), SA_{NOT} as 0.901 (SE: 0.067; 95% CI: 0.672–0.980) and S_{INT} as 0.966 (SE: 0.031; 95% CI: 0.819–0.994).

3.2.3. Population growth rate

Both models had similar AIC_c (Appendix A, Table A.2), with $\Delta QAIC_c < 2$, so a model averaging was applied. Population growth rate was positive for INT animals at 1.039 (SE: 0.025; 95% CI: 0.986–1.091), which is equivalent to a 4% growth rate. On the other hand, the rate was almost stable for NOT pods at 0.995 (SE: 0.053; 95% CI: 0.832–1.159) (Appendix A, Table A.2).

3.2.4. Reproductive rates

A female that was born in 2000 gave birth to her first calf in 2011 (11 years old). Mean calving rate estimated for INT was 0.219 (SE = 0.034), higher than for NOT with 0.020 (SE = 0.013) (Appendix A, Table A.3). This difference was significant (Mann–Whitney–Wilcoxon test, $W = 94$, $p = 0.001$). Only two births from different females were documented within NOT, so calving interval and fecundity rate were not estimated. Within INT, we documented 13 births. However, only 2 intervals between viable calves of 2 females were observed and ranged from 6 to 8 (mean = 7) years, producing a fecundity rate of 0.14 calves per year (Appendix A, Table A.3).

3.3. Interactions with the drop-line fishery

Data on Spanish and Moroccan catches from tuna drop-line fisheries were available from 2000–2011. Between 2000 and 2004 the average annual catch was 604 tons, followed by a sharp decline with an average annual catch of 123 tons between 2005 and 2010 (Fig. 2). At the same

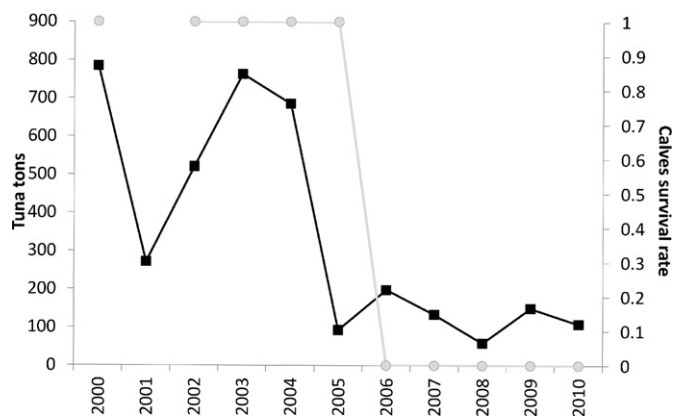


Fig. 2. Relationship of tuna captured by drop-line fisheries and SC_{INT} . In black drop-line catches and in grey SC_{INT} .

time, a dramatic change in calf survival of the INT pods was observed in 2006 (Fig. 2). The model that better explained the evolution of SC_{INT} was tuna catch by the drop-line catches the previous year (lag1; $\chi^2 = 8.48$, $df = 1$, $p = 0.004$) (Table 1). When we applied the values from the NRKW population, we obtained 573 tons of tuna catches for a calf survival of 0.91 (stable), and 687 tons for 0.97 (unrestrained growth) (Fig. 3).

In 2004, 48 boats composed the Spanish fleet of the drop-line fishery and 597 tons of tuna were landed in the harbour of Tarifa. According to interviews, at least 117 tuna were lost due to operational causes, described as lines cut by other vessels, tuna that escaped from the hook by itself or were let go by the fishermen, because fishermen could only haul one tuna at a time, so if two fish were hooked, they had to let one go free. On the other hand, 42 tuna were depredated by killer whales and 6 were bitten. In 2004 the average weight of tuna landed in Tarifa was 187 kg. Therefore, 42 depredated tuna weighed approximately 7869 kg and 6 bitten tuna weighed approximately 779 kg. In total about 8648 kg of tuna were provided to the killer whales by the interaction with the drop-line fishery in 2004.

3.4. Energetic requirements of killer whales

Two stranded whales were recorded in the Strait during the study period: a female in 2005 in Algeciras, Spain, measuring 5.7 m (Guinet et al., 2007), and another female in 2015 near Tangier, Morocco, measuring 5.53 m (INRH, see Appendix A, Table A.4). Consistently, the average total length of killer whales captured or stranded in nearby waters was 5.3 m for females and 6 m for males (see Appendix A, Table A.4). After applying the length-at-age and energy consumption models of Williams et al. (2011), we calculated daily and annual tuna consumption for INT pods in 2004 consisting of 14 animals, 2 adult males, 7 adult females, 4 juveniles and 1 calf (the calf was not considered in this analysis, because it was still feeding on maternal milk). These pods required a total mean of 1.0×10^6 kcal per day, which would be provided by capturing 21 to 141 tuna per day of 1.5 to 0.8 m respectively, while actively hunting. Thus, they would require 539 tons annually. Conversely, when given access to larger tuna (2 m) through depredation, the same whales only needed to eat up to 8 fish per day and would need 92 tons in the summer season. We then calculated the tuna consumption for all pods in 2011 for a total of 39 killer whales, including 9 males, 23 females, 4 juveniles and 3 calves (also not considered in the analysis, see Appendix A, Table A.5). We estimated that the whole community required about 3.2×10^6 kcal per day, for which they would need to capture 66 to 434 tuna per day from 1.5 to 0.8 m respectively, while actively hunting. In total, the community would have required 1654 tons of tuna in 2011.

4. Discussion

We have described a small community of 39 killer whales that are at least seasonally resident in the Strait. The asymptotic tendency of the discovery curve of individuals (Fig. 1) indicates that most of the identifiable proportion of this community is included in the catalogue, and lends confidence to the complete enumeration over time as a rigorous cumulative abundance count (Reisinger et al., 2011). It is a small

Table 1

Summary of the models used to estimate the relationship between annual calf survival rate SC_{INT} and tuna drop-line catches of Spain and Morocco combined during the same year (lag0), one year before (lag1) or two years before (lag2); significant terms ($p < 0.05$) are indicated by an asterisk.

Parameter	p -Value	df	AIC_c	ΔAIC_c
lag1	0.004*	1	−6.478	0
lag0	0.012*	1	−4.331	2.147
lag2	0.033*	1	−2.561	3.917

* $p < 0.05$.

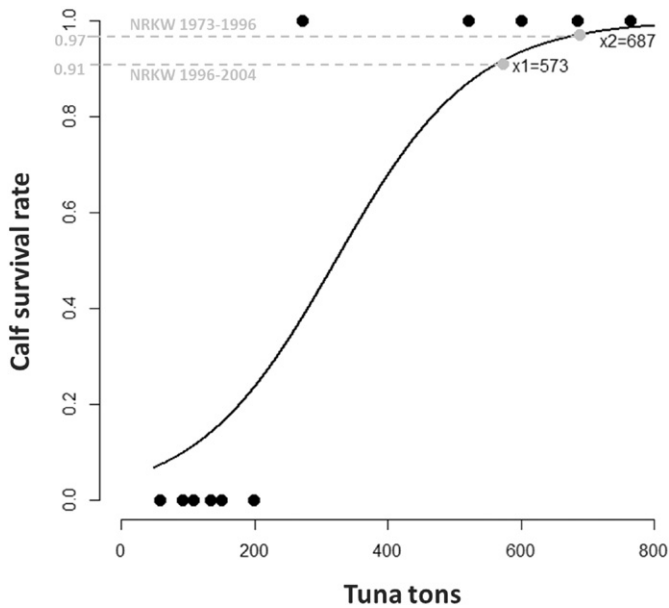


Fig. 3. Firth's logistic regression of calf survival rate and the tuna captured the previous year by the drop-line fishery. X1 calculated at a $SC_{INT} = 0.91$ and X2 estimated at $SC_{INT} = 0.97$, calf survival rates for northern resident killer whales (NRKW) at a different study period.

community compared to estimates of 115 to 1500 individuals in other populations (Visser, 2000; Hoelzel et al., 2007; Matkin et al., 2008; Ivkovich et al., 2010; Foote et al., 2010; Ellis et al., 2011; Matkin and Durban, 2011; Beck et al., 2012; Kuningas et al., 2013), but as with other small populations is considered to be declining (Barrett-Lennard and Heise, 2006; Matkin et al., 2008; Poncelet et al., 2009; Foote et al., 2010; Reisinger et al., 2011; Young et al., 2011; Häussermann and Acevedo, 2013; Beck et al., 2013; Lawson and Stevens, 2013).

There are demographic differences between INT and NOT pods. Both adult survival rates were similar to other populations (Olesiuk et al., 1990; Olesiuk et al., 2005; Poncelet et al., 2010; Kuningas et al., 2013; Matkin et al., 2014), but INT adults presented higher survival rates than NOT (Appendix A, Table A.3). Similarly, the INT calving rate was significantly higher than NOT (Appendix A, Table A.3), and only one calf and one juvenile were ever observed within NOT pods. While the calving rate for INT was similar to other killer whale populations (Olesiuk et al., 1990; Matkin et al., 2014; Tixier et al., 2014), calving rate for NOT was even lower than non-depredating individuals in the Crozet Islands (Tixier et al., 2014), a population considered to have a very low reproductive output. Calving interval and fecundity rate, calculated only for INT, were respectively longer and lower than for other populations considered in good condition (Olesiuk et al., 1990, 2005; Kuningas et al., 2013; Matkin et al., 2014) and very similar to the values estimated for Crozet (Tixier et al., 2014). These low parameters are mainly due to the high mortality of INT calves after 2005.

The population growth rate was positive for INT and similar to the NRKW (Olesiuk et al., 1990, 2005). In southern Alaska, the resident population growth rate was estimated at 3.5%. This population is considered to have reached a maximum growth rate thanks to the increasing return of their main prey (Matkin et al., 2014). Conversely, NOT pods are just below stable growth rate, with almost no recruitment over 12 years and a lower adult survival, putting them at greater risk due to the already very low number of animals within these pods (21 individuals). The situation is similar for the AT1 transient killer whales in Alaska, a group of only 7 individuals, which has had no recruitment since the Exxon Valdez oil spill in 1984, putting them on the verge of extinction (Matkin et al., 2008, 2012). However, population dynamics in long-lived vertebrates are often the least sensitive to variation recruitment (Sherley et al., 2015). For example, in African penguins (*Spheniscus*

demersus), chick survival was 18% higher when the sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) fisheries stopped for 3 years. The population continued to decline, probably because of high adult mortality linked to poor prey availability over a larger spatial scale, as the regional abundance of sardine fell below a critical threshold (Sherley et al., 2015).

Eastern tuna stocks have been declining since the 1980s (ICCAT, 2011; Taylor et al., 2011). In 1998, the International Commission for the Conservation of Atlantic Tunas (ICCAT) established a Total Allowable Catch (TAC) and national quotas that are attributed to contracting parties (ICCAT, 2011). Each member country then distributes percentages of their national quota among the different fishing fleets. However, from the late 1990s to 2008, the ICCAT did not follow the recommendations of its own Scientific Committee (Fromentin et al., 2014) and additionally, tuna catches were seriously under-reported, likely causing the stock decline over that period. Between 2009 and 2011, the ICCAT fully endorsed the scientific guidance and recommended a low TAC around 18,500–22,000 t (ICCAT, 2014). As a result, the most recent assessments show signs of biomass increase after 2011 (ICCAT, 2014). Killer whales in the Strait clearly depend on tuna abundance, as their main prey (García-Tiscar, 2009), and thus we suggest that the efforts undertaken by ICCAT in the past years be continued to ensure that the Eastern Stock of tuna fully recovers and remains above Maximum Sustainable Yield (MSY) levels.

Marine predators are most sensitive to changes in fish abundance when prey abundance is low (Cury et al., 2011). In this study a small community of killer whales may have suffered from the decline of eastern tuna stocks since the 1980s. Stocks improved in the 1990s, when they reached half the initial stock size (Taylor et al., 2011) and the drop-line fishery began operating in 1995. This may have presented an opportunity to some pods to overcome the low tuna abundance via depredation, and to ensure the recruitment of young animals into the pods through numerous births and a high calf survival rate. However, when the stocks reached their lowest levels after 2005, declining below MSY (Taylor et al., 2011), even depredating pods could not cope with the very low prey availability, and as a result, the recruitment stopped.

Depredation is a good opportunity for killer whales to feed because in summer, when tuna are crossing the Strait on their way to the Atlantic, they prefer deep waters (Wilson and Block, 2009). This tuna would thus be unreachable to killer whales. However, drop-line fisheries bring tuna to the surface and could be acting as an accumulator of fish, locally increasing the availability of tuna. This is especially important for killer whales when the abundance of tuna is low. In that case, food provisioning through depredation could have highly affected killer whales' life-history parameters in the years in which the tuna stock was at its lowest. Since 2005, drop-line catches declined dramatically, reflecting the decline of tuna abundance. Since 2006, one year later, none of the killer whale calves have survived in the Strait as of 2011. This relationship between calf survival and tuna catches as a proxy of tuna abundance highlights the importance of artificial food provisioning in times when prey is scarce. In these low abundance years, calf survival depended on the mother's access to sufficient depredated tuna the year before it was born. We recorded 42 tuna caught on Spanish drop-lines in 2004 as depredated by killer whales, and 6 tuna bitten, representing a total of 8648 kg of tuna. Other authors have also studied this interaction and their results are consistent with ours; De la Serna et al. (2010) estimated that on average 15 tuna landed annually in Tarifa between 1998 and 2007, and presented unequivocal signs of depredation by killer whales (only individuals bitten, not completely depredated), but in 2005 zero tuna were bitten. Moreover, Malouli Idrissi et al. (2013) reported that killer whale depredated 5794 kg of tuna from Moroccan drop-lines in 2009 and none in 2010.

Minimum drop-line catches of 573 tons would allow SC_{INT} similar to that observed in healthy populations such as the NRKW (Olesiuk et al., 1990, 2005). Until 2004, tuna drop-line catches exceeded this minimum and the calves born until 2005 survived. No calves born after this year

survived to their first year of life, when the catches were below this limit. Additional factors should be taken into account. If pregnant and lactating females did not have access to enough tuna to meet their energy requirements, then food deprivation promotes the metabolism of lipid stores, releasing sequestered pollutants into circulation (Aguilar et al., 1999; O'Shea, 1999). This could be discharged into suckling calves via lactation and affect the offspring survival. Although high levels of pollutants were found in other populations of free-ranging killer whales (Ross et al., 2000; Rayne et al., 2004; Hickie et al., 2007), no information is available on contaminants in killer whales from the Strait. We could hypothesize that food deprivation may have affected the survival of calves when drop-line catches were at a minimum. Moreover, tuna sampled in the area presented high levels of pollutants (Sprague et al., 2012), and thus whales are already mainly feeding on contaminated prey. The interaction with the fishery seems to improve killer whale breeding capacities, as we found significant differences between INT and NOT calving rates. Tixier et al. (2014) found a positive effect of depredation in long-line fisheries on female calving rate at the Crozet Archipelago, suggesting an effect of artificial food provisioning on female reproductive output. Artificial food provisioning by the fisheries would provide sufficient energy to INT whales to reproduce. When the energy gained during pregnancy was high enough, it would support the survival of the calf.

We should note that the energy requirements estimated here may be biased. First, length measurements were based on values calculated from past stranded and captured whales. However, these values are similar to the length of the animals used to measure energetic requirements by Williams et al. (2011), with an 80th percentile of 5.6 m for females and 6.04 m for males. Secondly, there was no information available on the diet composition of these killer whales in winter or autumn. Finally, we were not able to take into account the fact that while actively hunting, killer whales would presumably consume more energy than when interacting. Killer whales have different energy costs depending on activities and swimming speeds. Nevertheless, the energy cost is generally low in this species (Williams et al., 2002, 2006; Williams and Noren, 2009). When whales are depredating on drop-lines, they are patrolling the fishing vessels, waiting for tuna to get hooked on the line (Esteban et al., 2015). On the other hand, during active hunting, they are chasing tuna for about 30 min at high speed (Guinet et al., 2007). Presumably, depredation should have a lower energy cost than active hunting, conferring an advantage on depredating whales. Moreover, depredation via interaction with drop-line fisheries provides access to larger tuna. Thus, depredation would provide more energy and at a lower cost.

The Strait is a high-noise area as a result of intense marine traffic, 112.5 dB re: 1 μ Pa rms, 10–585 Hz (Castellote et al., 2012). This may affect the distribution and availability of tuna, as tuna are very sensitive to noise and show an escape response to the presence of shipping noise similar to anti-predator behaviour (Sarà et al., 2007). Noise could also affect killer whale communications and their ability to actively hunt (Foote et al., 2004; Williams et al., 2014). Vessel traffic may result in whales changing their behaviour (Williams et al. 2002, 2006).

To maintain the equilibrium between killer whales, tuna and human activities in the Strait, in 2011, the Spanish Ministry of Environment included the killer whales in the vulnerable category in the Spanish catalogue of endangered species (R.D. 139/2011). This categorization requires a conservation plan to be created within 5 years. Based on the information presented in this study, we strongly recommend that killer whales in the Strait be included as endangered in the Spanish catalogue of endangered species under criteria A2 (reduction in population size), C1 (small population size) and D (expert judgement). Moreover, a conservation plan is urgently needed. The recovery of tuna above MSY levels will be especially important to the conservation effort of killer whales in the Strait. We therefore suggest that tuna stock assessment would greatly benefit from the implementation of an Ecosystem-based fishery management programme (Pikitch et al., 2004), in which

ICCAT consider all of its predators when setting TACs and country-specific quotas: humans, killer whales and sharks. Ecosystem-based fishery management is a new approach to fishery management, essentially reversing the order of management priorities to begin with the ecosystem rather than the target species (Pikitch et al., 2004). We think that a specific quota of tuna should be allocated to killer whales, corresponding to the energy requirements of part or the whole community or their energy needs should be included in tuna natural mortality assessment. We estimated that in 2011, INT would need 539 tons of tuna and all individuals would need 1654 tons. TAC for eastern tuna was set at 18,500 tons in the same year, so the needs of whale would represent from 3 to 9% of the TAC. A similar proposal was put forth for the recovery of SRKW where the whales would get a salmon catch allocation under the Pacific Salmon Treaty (Williams et al., 2011). This would require a yearly assessment of the killer whale community to be performed prior to the attribution of national quotas by ICCAT.

To cope with management of shared fish stocks as bluefin tuna, Marine Protected Areas (MPAs) could be a useful policy instrument (Sumaila and Huang, 2012). MPAs are areas in the ocean where different human activities are regulated more stringently than elsewhere. Because tuna congregate to spawn, they are highly vulnerable to commercial fishing at their spawning times, where the major gear to catch them is currently operating (Fromentin et al., 2014). So ideally MPAs where fishing is not allowed should be placed in tuna spawning area, as a no-take marine reserve (Costello, 2014), but spawning happens inside the Mediterranean, which is out of the scope of this study. Therefore, we propose the creation of a seasonal management area in spring when killer whales are actively hunting (Appendix A, Fig. A.1) where the ancient and sustainable fishing gear of trap net is allowed but disturbance activities, for both killer whales and tuna, should be limited including navy exercises, seismic surveys and even whale-watching and sport-fishing activities. This seasonal management area should be aimed to increase the ability of killer whales to actively hunt tuna from March to August.

As a short-term urgent action, we also propose that Spain and Morocco transfer a higher percentage of their national quota for artisanal drop-line and trap-net fisheries in the Strait versus industrial purse-seiner fisheries in the Mediterranean Sea, at least until the killer whale community show clear signs of stability and recovery.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2015.11.031>.

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