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Mathematical models of long term evolution of blue whale song types' frequencies



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ABSTRACT

The linear decrease in the frequency of blue whale songs around the world is, to date, an unexplained phenomenon. We show it can be reproduced by a mathematical model considering two antagonistic behavioral trends: first, a bias towards conformity in the song, and second, a tendency to try and sing lower than the other whales. We check the robustness of our model by considering some more complex premises. First, different hierarchical relations between the singers are explored, adapting methods used in the flocking motion studies. Then a population-dependant simulation shows that even considering the gradual addition of new whales, the evolution is still globally linear. Finally, we show that intra-annual variations surging from different causes can be naturally incorporated into the model. We then conclude that, unlike other explanations, a cultural hypothesis seems compatible with the observed linearity of the blue whales's songs frequency shift.

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1. Introduction

Blue whales (*Balaenoptera musculus*) emit stereotyped vocalizations called 'songs', of which ten geographically distinct types have been recognized worldwide (McDonald et al., 2006). A linear decrease of the frequency of these songs has been shown by McDonald et al. (2009). Since this pioneer paper, a number of studies have confirmed this linear trend, such as Gavrilov et al. (2012) (Antarctic ocean blue whale), Miller et al. (2014) (pygmy blue whales, South West Pacific ocean) (Leroy et al., 2018; Miksis-Olds et al., 2018; Cerchio et al., 2020; Leroy et al., 2021) (pygmy blue whales, Indian ocean, different types of song) or Malige et al. (2020) (pygmy blue whales, South East Pacific blue whale), with sometimes an additional intra-annual variation of the songs (Gavrilov et al., 2012; Leroy et al., 2018). The cause of this regular decrease in the song's frequency remains unclear, while several hypothesis have been mentioned, such as: a post-whaling augmentation of the whales density, the influence of underwater noise contamination, an increase in the average size of the whales due to post-whaling recovery, a propagation effect in an ocean more acid due to climatic change (McDonald et al., 2009), a change in

the average depth of song emission (Gavrilov et al., 2011). None of these hypothesis however, is able to explain satisfactorily the main characteristics of this phenomenon that we list thereafter. First, the decrease is extremely regular even in a long timescale, of more than 50 years (McDonald et al., 2009). This means that, even if another mathematical function lies below the change in frequency (such as the more classical exponential or sinusoidal functions, rather common in physical phenomena), then it evolves so slowly that the function can be assimilated to a portion of straight line for the timescale that we consider. Such a linear decrease has been measured for all the geographically distinct types of song, and, inside these songs, for all the studied units (Malige et al., 2020). It is very difficult to find a cause of physical, physiological or anthropogenic nature evolving as a straight line at this timescale: the average ambient noise, size of the whales, density of populations, pH and temperature of the ocean, all have more complex or more rapid changes with time (Feely et al., 2009; Rohde and Hausfather, 2020), that cannot be assimilated to a portion of straight line in this timescale. What's more, no visible influence of local parameters such as a locally noisy ocean or a higher density of whales has been found (Gavrilov et al., 2011; Leroy et al., 2018; Miksis-Olds et al., 2018). Finally, the decrease in frequency is sometimes different for each song unit in a single song (Miksis-Olds et al., 2018; Malige et al., 2020; Cerchio et al., 2020).

Blue whale songs are possibly linked to reproduction, since only males have been found to emit this type of vocalization (Oleson

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¹ <https://www.cogitamus.fr/manifesteen.html>.

et al., 2007). In this context, the songs frequency decrease could be due to cultural interactions, and emerge as a compromise between two opposite tendencies, as proposed by Malige et al. (2020): a reproductive advantage linked to low frequency song emission, counterbalanced by a cultural conformity to the group. Thus, any individual would try to emit lower than the rest of the acoustical group, while keeping as close to it as possible, and a collective and visible behaviour would emerge from simple individual behaviours.

Modelling the emergence of a collective effect from simple behaviours of individuals (bottom-up agent based models) has become an important tool in theoretical biology. While numerical models are usually employed in cetacean studies (Filatova and Miller, 2015; Mccloughlin et al., 2018; Zandberg et al., 2021), important efforts have been deployed to use mathematical modelling for flocking motions (Fine and Shell, 2013). Most of these models study the evolution of the position and velocity of each individual through differential equations or by techniques of statistical physics. The differential equations usually feature an attraction component (at long range) and a repulsion one (at short range) between the agents, inducing the stabilization of the trajectories towards a collective 'averaged' motion, much more simple than the initial individual movements (Tanner et al., 2003). The same family of mathematical models was used for modelling language evolution (Cucker et al., 2004), but also communications through control theory in engineering (Beard and Stepanyan, 2003) and the search for consensus in social networks (Ren and Beard, 2007; Proskurnikov and Tempo, 2017). This last application is particularly interesting when we consider, following Tyack (2008), that the search for consensus in vocal production is a mean of providing cohesion in social groups for different animal species. To our knowledge, no attempt has yet been done towards using mathematical modelling to explain the evolution of blue whales' songs.

In this work we test the hypothesis of a cultural origin of the frequency decrease of whales songs by mathematically modelling two contradictory impulses in individuals, one towards low frequency singing, and the other towards conformity in the social group. First we describe our simple mathematical model, a set of differential equations in which the unknown functions are the songs frequencies of each individual, varying with time. Mathematically resolving this set of differential equations leads to a collective asymptotic behaviour that is a linear function of time. We then try the robustness of our model by considering the results of more complex interactions between singing whales. A comparison between the model's predictions and actual data is then discussed. We give most of the mathematical proofs as supplementary materials, available on-line.

2. Biological hypothesis

We seek to test the result, visible at the community level, of two different trends in the singing whales behaviour:

- each individual wants to sing lower than other whales,
- each individual wants to sing at a frequency as close as possible to the group's general behaviour.

The first trend is suggested by studies in other species, where low frequency vocal emissions can be linked to an increase in mating success (Searcy and Andersson, 1986). The blue whale song production is probably of a source-filter type (Reidenberg, 2017; Patris et al., 2019). In numerous species producing vocalizations of this type, and especially in mammals, the song's peak frequencies (selected by the formants of the vocal filter) and fundamental frequencies are positively correlated with the size of the vocalizing

system, which is itself correlated with the size of the animal (Pfefferle and Fischer, 2006; Sanvito et al., 2007; Reby et al., 2010; Martin et al., 2016). In some species, low frequency vocalizations of males have been shown to be linked to dominant positions (Vannoni and McElligott, 2008) or enhanced attraction of females (Searcy and Andersson, 1986). It is not a general rule however, since more complex situations have also been documented (Reby et al., 2010). Because blue whales are such a difficult species to study, no evidence exists that for this species, low frequency vocalizations are linked to a reproductive advantage. We consider, however, that it is a plausible hypothesis, consistent with the marked gigantism of the species. Any "cultural drive", not specially linked to reproduction, could also be the reason for the tendency to sing lower in frequency (Whitehead and Rendell, 2015, page 89).

The conformity trend is mainly suggested by the very striking similarity of songs among blue whales individuals of a given acoustical group (Hoffman et al., 2010; Leroy et al., 2018; Patris et al., 2019). To this day, no study has been able to distinguish the songs of two separate singers. Moreover, the importance of cultural conformity has been stressed in several species (Tyack, 2008; Aplin et al., 2014; Bridges and Chittka, 2019), especially for species facing a large geographical dispersion (Tyack, 2008). Conformity bias has been shown to have a stabilizing effect for bird songs (Lachlan et al., 2018). Imitation of other individuals is thought to be the source of homogeneity in song production among several species of cetaceans (Tyack, 2008; Mccloughlin et al., 2018); Hoffman et al. (2010) suggested that the strict homogeneity of song in blue whales acoustic groups could help them localizing each other.

The two contradictory impulses will be summarized in one general hypothesis for the agent's behaviour:

- each individual tries to sing slightly lower than the average of the acoustical group. (*H*)

3. Mathematical modelling

3.1. Model design

We consider a very simple linear set of differential equations to model the action of the hypothesis (*H*). Let $F_1(t), F_2(t), F_3(t), \dots, F_n(t)$ be the characteristic frequencies of the songs of the n whales, each frequency being a function of time. The $F_i(t)$ can be peak frequencies, or fundamental frequencies of a song unit, depending on what parameter best represents the song (Patris et al., 2019). The (*H*) hypothesis can be modelled by the following differential equations, for each whale i , along with the initial value $F_i(0)$:

$$\frac{d}{dt}F_i(t) = -a(F_i(t) - (\bar{F}(t) - \Delta F_i)) \quad (1)$$

where $\bar{F}(t) = \frac{1}{n} \sum_{i=1}^n F_i(t)$ is the average of the n frequencies, and a is a positive coefficient indicating the strength of the acoustical influence between the whales. The coefficient a is chosen identical for all whales in a first simple model (in Section 4.1 the influence of relaxing this constraint on a is discussed). ΔF_i is a positive coefficient characteristic of the whale i , and we suppose that $\Delta F_i \ll \bar{F}(t)$. Thus, Eq. 1 shows that the whale i tends to changing its song's frequency so that it reaches a value of $\bar{F}(t) - \Delta F_i$, slightly lower than the average of the group.

3.2. Mathematical resolution

The resolution of Eq. (1) is explained in details in the supplementary materials. The main difficulty arises from the coupling

of the n equations via the averaging of all frequencies. We obtain the following expression for each frequency:

$$F_i(t) = \bar{F}_0 - (\Delta F_i - \bar{\Delta F}) - (a\bar{\Delta F}) t + e^{-at} (F_i(0) - \bar{F}_0 + \Delta F_i - \bar{\Delta F}) \quad (2)$$

where $\bar{F}_0 = \frac{1}{n} \sum_{i=1}^n F_i(0)$, $\bar{\Delta F} = \frac{1}{n} \sum_{i=1}^n \Delta F_i$.

The term $e^{-at} (F_i(0) - \bar{F}_0 + \Delta F_i - \bar{\Delta F})$, which denotes a difference between the individual characteristics and the averaged ones, is attenuated with a characteristic time of $\tau = \frac{1}{a}$. The asymptotic behaviour of the solution $F_i(t)$ is thus:

$$F_i(t) \underset{t \gg \tau^{-1}}{\sim} \bar{F}_0 - (\Delta F_i - \bar{\Delta F}) - (a\bar{\Delta F}) t \quad (3)$$

The function in Eq. (3) is a straight line for which the y-intercept is dependant on the whale (through the difference between individual ΔF_i and averaged $\bar{\Delta F}$) but the slope is not. The differences between y-intercepts are low, since the ΔF_i have been supposed much smaller than \bar{F}_0 . This means that after a while each whale tends to lower its frequency in a linear function of time. All the whales that are in acoustic interaction lower their song with the same rate $a\bar{\Delta F}$, following parallel straight lines that are almost merged.

Fig. 1 gives some example of the frequency decline of 5 acoustically-related whales. We can see that the convergence towards linear comportments is linked to the strength of mutual influence a . On the small graphs of Fig. 1, for values of $\frac{\bar{\Delta F}}{\bar{F}_0} \lesssim 4\%$, the linear asymptotes are almost indistinguishable.

3.3. Matrix formulation

We can rewrite the system of Eq. (1) in a vectorial form, involving matrices. Let $\mathbf{F}(t) = {}^t(F_1(t), F_2(t), F_3(t), \dots, F_n(t))$ be the vertical vector of \mathbb{R}^n representing the n frequencies (where the t symbol denotes the transpose of a vector or a matrix). Let $\Delta \mathbf{F} = {}^t(\Delta F_1, \Delta F_2, \Delta F_3, \dots, \Delta F_n)$, \mathcal{U} is a $n \times n$ matrix containing only the value 1, and \mathcal{I} the identity matrix of rank n . We can rewrite the system (1) as the following vector valued differential equation:

$$\frac{d}{dt} \mathbf{F}(t) = -a \left(\mathcal{I} \mathbf{F}(t) - \frac{1}{n} \mathcal{U} \times \mathbf{F}(t) + \Delta \mathbf{F} \right) = -\mathcal{L} \times \mathbf{F}(t) - a\Delta \mathbf{F} \quad (4)$$

with $\mathcal{L} = a(\mathcal{I}d - \frac{1}{n}\mathcal{U})$. The entries of the matrix \mathcal{L} are thus, for $i \neq j$, $\mathcal{L}_{ij} = -\frac{a}{n}$ and $\mathcal{L}_{ii} = \frac{a(n-1)}{n}$. We notice that \mathcal{L} has negative values except in the diagonal, and that the sum of the elements in a line is zero. In general, such a matrix is called a Laplacian matrix and can be used to represent a weighted directed graph, $-\mathcal{L}_{ij}$ being the weight of the transition from node j to node i (for $i \neq j$) (Agaev and Chebotarev, 2005). In our case, the graph \mathcal{G} would have n nodes representing individual whales, and n^2 edges with the weight $\frac{a}{n}$ representing the relation between each two whales.

4. Robustness of the model to more complex behaviours

4.1. Varying the interaction between whales

The matrix formulation presented in Section 3.3 gives a clue to generalizing the model. Instead of supposing that $\frac{a}{n}$ is the universal factor of influence between two individual whales, we can imagine that whale j has an influence over whale i characterized by the positive factor a_{ij} and that the whale i tries to be ΔF_{ij} under the frequency of whale j . Thus, Eq. 1 generalizes to:

$$\frac{d}{dt} F_i(t) = - \sum_{j=1}^n a_{ij} (F_i(t) - (F_j(t) - \Delta F_{ij})) \quad (5)$$

This equation can also be expressed as a vector valued differential equation. By letting $\mathbf{S} = {}^t(S_1, S_2, \dots, S_n)$ be the vector such that $S_i = \sum_{j=1}^n a_{ij} \Delta F_{ij}$ and \mathcal{L} the Laplacian matrix such that $\forall i, \mathcal{L}_{ii} = \sum_{j \neq i} a_{ij}$ and for $j \neq i, \mathcal{L}_{ij} = -a_{ij}$, we have:

$$\frac{d}{dt} \mathbf{F}(t) = -\mathcal{L} \times \mathbf{F}(t) - \mathbf{S} \quad (6)$$

Then, \mathcal{L} has negative values except on its diagonal, and the sum of its elements on a line is zero. \mathcal{L} is the Laplacian matrix representing the graph of acoustic interactions \mathcal{G} where the weight of the directed edge between whale (node) j and whale (node) i is now a_{ij} : a_{ij} represents the strength by which the whale i is taking into account the frequency of the whale j to change its own frequency.

Eq. (6) has been extensively studied in flocking models studies (Cucker and Smale, 2007). \mathcal{L} has several very important properties and is related to the topological characteristic of the graph (Ren et al., 2004; Cucker and Smale, 2007). Let's remind some simple topological properties of directed graphs that are of interest for our model (see also Proskurnikov and Tempo, 2017 for a good summary).

A walk connecting node i to node j is a pathway from node i to node j following directed edges (there exists a directed edge between k and l when a_{lk} is strictly positive). A root is a node connected by at least one walk to every other node in a graph. A graph is called *strongly connected* when there is a walk between any two of its nodes (thus, every node of a strongly connected graph is a root). A graph is called *quasi-strongly connected* if one of its node at least is a root (Fig. 2).

We can then use the Gerschgorin theorem (Gerschgorin, 1931) and adapt the work of Ren et al. (2004) to prove the following result:

Theorem 1. *If the graph \mathcal{G} associated to \mathcal{L} is quasi-strongly connected, then the frequencies of the n whales tend to linear functions with a common slope V . In the general case, the expression of the slope V can be obtained from the reduction of \mathcal{L} to its normal Jordan form*

(mathematical proofs and more details are given in the supplementary materials).

If the graph is not quasi-strongly connected, then this result does not hold. The meaning of a quasi-strongly connected acoustical group of whales can be interpreted thanks to the Fig. 2. Each arrow represents acoustical information going from whale j to whale i . In the graph on the left, we can see that every whale receives information (possibly through other whales) from whale 1. Thus, a song produced by whale 1 will reach every other whale. We call this a group of acoustically connected whales. On the contrary, in the graph on the right (not quasi-strongly connected), we can find two whales (whale 1 and whale 5) that are not 'acoustically related' in the sense that none receive information from the other, even through other whales. There is no whale, in this graph, that can influence all the rest of the group.

An important consequence is that a whale or group of whales that are separated from all the others will not tend to follow the general trend of other whales and will converge toward their own asymptote. In Section 5, we discuss this point as being one of the few observable phenomenon that could disconfirm our hypothesis.

In the following paragraphs, we examine a few special cases of interest, considering always a quasi-strongly connected graph, that is to say a group of whales acoustically coherent.

Case (a): symmetric interactions. We suppose that, for all (i, j) , $a_{ij} = a_{ji}$. Thus, influence of whale i over whale j is the same that influence of whale j over whale i . A classical example of such

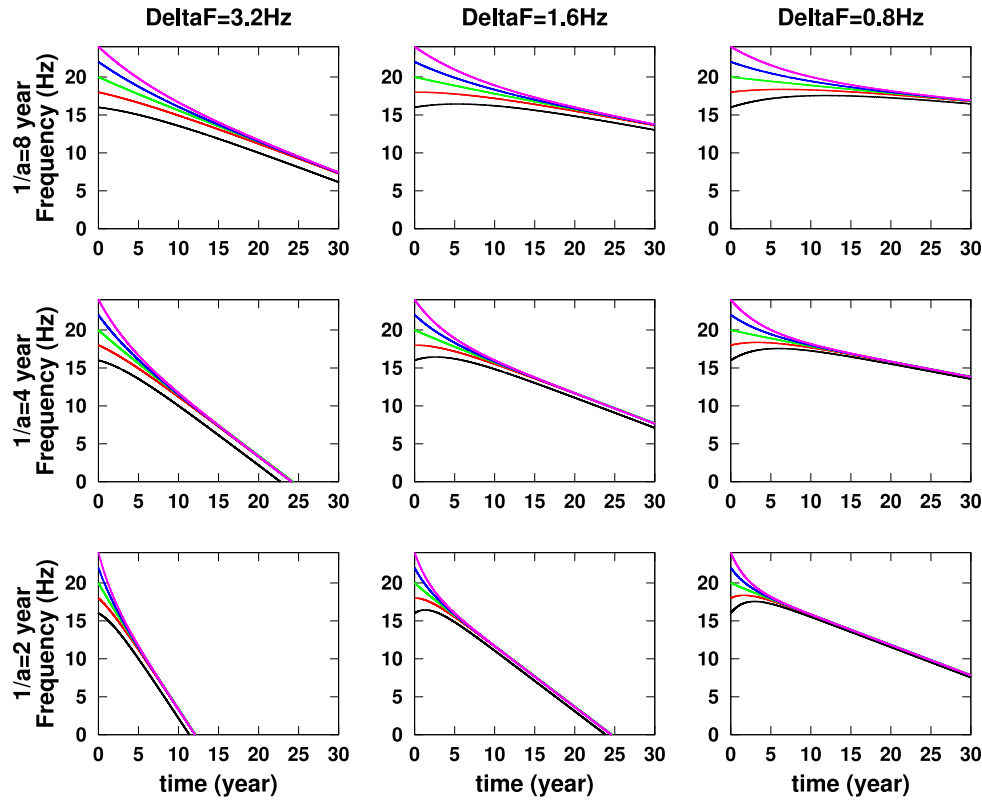


Fig. 1. Examples of frequency decline for 5 whales, from the simple model given by Eq. (1). Initial values $F_i(0)$ are chosen as 16 Hz, 18 Hz, 20 Hz, 22 Hz and 24 Hz to represent plausible values for blue whales. Parameters a and ΔF vary to show distinct behaviours, a being constant for each line and ΔF for each column. Individual ΔF_i are randomly chosen with a Gaussian probability function with standard deviation $\sigma_{\Delta F} = 0.3$ Hz and mean value ΔF as shown, in each column.

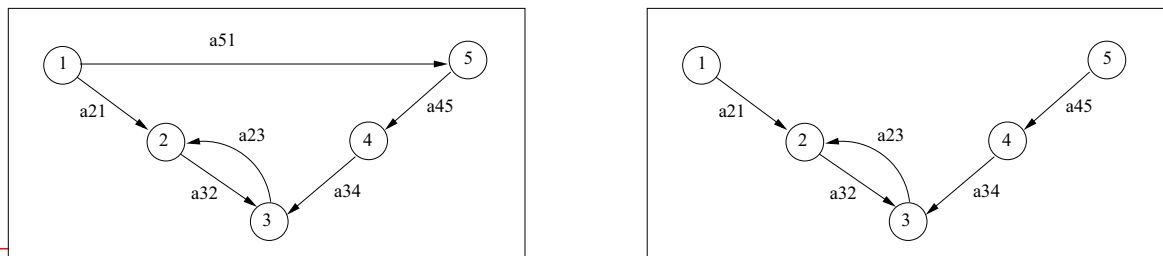


Fig. 2. Examples of directed graphs. We represented an edge from node j to node i only if a_{ij} is not equal to zero, i.e. when whale i takes into account the frequency of whale j to change its own frequency. Left, a graph that is quasi-strongly connected, with node 1 being a root of the graph. Right, the graph is not quasi-strongly connected.

reciprocal interaction is the case where the distance is the main factor affecting influence between two whales. In this case, the common slope of asymptotes is given by:

$$V_{\text{symmetric}} = -\frac{1}{n} \sum_{i,j=1}^n a_{ij} \Delta F_{ij} \tag{7}$$

Case (b): strictly hierarchical interactions. We suppose that, for all $j > i, a_{ij} = 0$. Thus, the interaction between any two whales is strictly asymmetrical: if whale j has an influence over whale i , then whale i has no influence over whale j (and then the whales have been 'organized' such as the more dominant is classed first, and so forth). In this case, the common slope of asymptotes is given by:

$$V_{\text{hierarchical}} = -a_{11} \Delta F_{11} \tag{8}$$

We see that asymptotically, all whales will copy the behaviour of the dominant whale.

Case (c): non-hierarchical individual case. We suppose that, for all $(i,j), a_{ij} = \frac{a_i}{n}$. Thus, whale i receive the same influence from every

whale j : a_i is characteristic of the 'sensibility' of whale i to the influence of any other whale. In this case, the common slope of asymptotes is given by:

$$V_{\text{sensitivity}} = -\frac{1}{n} \frac{\sum_{i,j=1}^n \Delta F_{ij}}{\sum_{i=1}^n (1/a_i)} \tag{9}$$

Case (d): hierarchical non-individual case. We suppose that, for all $(i,j), a_{ij} = \frac{a_j}{n}$. Thus, whale j will influence equally every whale i : a_j is characteristic of the 'power' of influencing of whale j , or dominance. In this case, the common slope of asymptotes is given by:

$$V_{\text{dominance}} = -\frac{1}{n} \frac{\sum_{i=1}^n a_i a_j \Delta F_{ij}}{\sum_{i=1}^n a_i} \tag{10}$$

Conclusion of varying the interaction between whales. We've seen that different interactions between the whales, as long as the group is acoustically coherent, always lead to a general behaviour of a linear descent. In practice, the individual parameters a_{ij} and ΔF_{ij} are not observable phenomena, thus, our model will not allow to distinguish between the possibilities that have been presented. In turn, we can see that if we admit the 'cultural hypothesis' (H), a large spectrum of individual relationships, from very hierarchical to very homogeneous, will lead to a linear descent. Our model is thus very robust to the type of individual interactions.

4.2. Forcing individual periodic variations

Several authors have shown that, in addition to the linear descent, the frequency of some of the blue whale songs vary with a period of one year (Gavrilov et al., 2012; Leroy et al., 2018). Leroy et al. (2018) argue that the reason for this yearly variation is possibly distinct from the reason for the linear descent. To include this observation in our model, one can simply suppose a yearly variation in the ΔF_{ij} . This yearly variation of the ΔF_{ij} could be due to environmental factors. As an example, one could assume that an increase of ambient noise (such as suggested by Leroy et al. (2018) due to ice melting) could drive the whales to enhance the difference with other whales (increase the ΔF_{ij}). Alternatively, the yearly variation of the ΔF_{ij} could be due to behavioural changes produced during the reproductive cycle, with a increase of the competition term in early spring.

The evolution of the system is now described by the following vector valued differential equation, a generalization of Eq. (6):

$$\frac{d}{dt} \mathbf{F}(t) = -\mathcal{L} \times \mathbf{F}(t) - \mathbf{S}(t) \quad (11)$$

The homogeneous equation is unchanged, and it can be proved (see supplementary materials) that if the functions ΔF_{ij} are T -periodic, the asymptotic solution is the sum of a linear decrease and a periodic variation of period T . An example of this solution is discussed in Section 5.3.

4.3. Influence of an evolving population

We now check the influence of an evolving population under our hypothesis: will the appearance of new singers, and disappearance of old ones, change the linear curve that we obtained? We developed a simple numerical model where a few initial individual whales reproduce at a determined rate, still with the interaction and behaviour described by the hypothesis (H).

Algorithm of the numerical model. The numerical model supposes a given lifespan for each singing whale (T_W) and a constant recruitment rate for the new singers (r). Each new year, we then consider the following events:

- disappearance of the singers that reached the lifespan limit from the population,
- introduction of the new singers, according to the recruitment rate, with an initial frequency given by a random distribution around the actual mean frequency of the group of singing whales,
- during the year, vocal interactions among the whales are modelled by Eq. (1).

The result of the modelling is a set of N vectors of individual frequencies (N is the total of all whales having participated). When the agent is not present among the community (because it is 'dead' or not yet 'born'), the frequency is conventionally set to 0. We then

plot the evolution of each non-zero frequency with time, along with the average frequency of the group and its standard deviation.

Set of chosen parameters for the numerical model. Our modelling is not fitted to a special acoustic group of whales, and is only meant to check a general robustness of the hypothesis. However, we tried to maintain the parameters of the numerical model realistic.

- Demographic parameters. The demographic model used is very simple and only considers a growth rate of the population due to the recruitment rate and the average lifespan.

- Lifespan (T_W): the average lifespan of blue whales has been estimated to about 80 years (Branch et al., 2007 mention a maximum age of 73 years). The age when males begin to sing is unknown, but Branch et al. (2007) estimated that sexual maturity does not happen before 10 years old or so. As a plausible value, we suppose a singer lifespan of $T_W = 60$ years.

- Recruitment rate (r): it is a parameter that is difficult to measure (Vernazzani et al., 2017). However, based on the work of Branch et al. (2007), we estimated a growth rate of about $r = 0.03 \text{ year}^{-1}$. The model is initiated with a number of whales equal to the integral part of $(1/r) + 1$ so as to ensure a viable population.

- Characteristics of the songs. The frequency of the song is defined like in our mathematical model: it can be a peak frequency or a fundamental frequency, whichever describes best a given song. The initial values are chosen in the order of magnitude of measured data (a few tens of Hertz).

- Distribution of initial frequencies: we chose a Gaussian random distribution centred on $\overline{F_0} = 35\text{Hz}$ with a standard deviation of $\sigma_{F_0} = 2\text{Hz}$. The new singers joining the population sing with a frequency randomly distributed around the actual group average and the same standard deviation of $\sigma_{F_0} = 2\text{Hz}$.

- Distribution of the parameters ΔF_i : this parameter, in our model, is the difference (compared to the group) to which is aiming the whale i . We supposed it small compared to F_0 . Here, we chose a Gaussian random distribution centered on $\overline{\Delta F} = 0.2 \text{ Hz}$, with a standard deviation of $\sigma_{\Delta F} = 0.02 \text{ Hz}$.

- Acoustic cohesion a : we chose a value of $a = 2 \text{ year}^{-1}$, corresponding to a converging time of about 6 months.

- Simulation parameters.

- Total duration (years): this parameters is chosen significantly larger than the lifespan of the agents. We chose to simulate the evolution over a duration of 250 years.

- Time step (year^{-1}): this is simply the number of points that will be computed per year. We fixed it to 12, to have some precision without having too large variables.

Results. Fig. 3 shows the evolution of the frequencies that we obtain. The general aspect is coherent: each new singer join the general trend in less than one year. The dispersion of the observed frequencies is now due to the dispersion of the 'apprentices'. As can be seen on Fig. 4, the average of the frequencies is evolving very close to a linear curve (Pearson coefficient of $R = 0.9994$). The standard deviation of the frequencies is variable but lower than 0.5 Hz (to be compared to the $\sigma_{F_0} = 2 \text{ Hz}$ for the new singers).

Another run of our simulation with more dispersion of the ΔF_i ($\sigma_{\Delta F} = 0.1 \text{ Hz}$) leads to similar results, with a Pearson coefficient of $R = 0.9995$ and a standard deviation lower than 0.4 Hz. Likewise, a run with a smaller group cohesion $a = 0.2 \text{ year}^{-1}$, corresponding to a convergence characteristic time of 5 years, gives the same general results with $R = 0.9992$ and a standard deviation

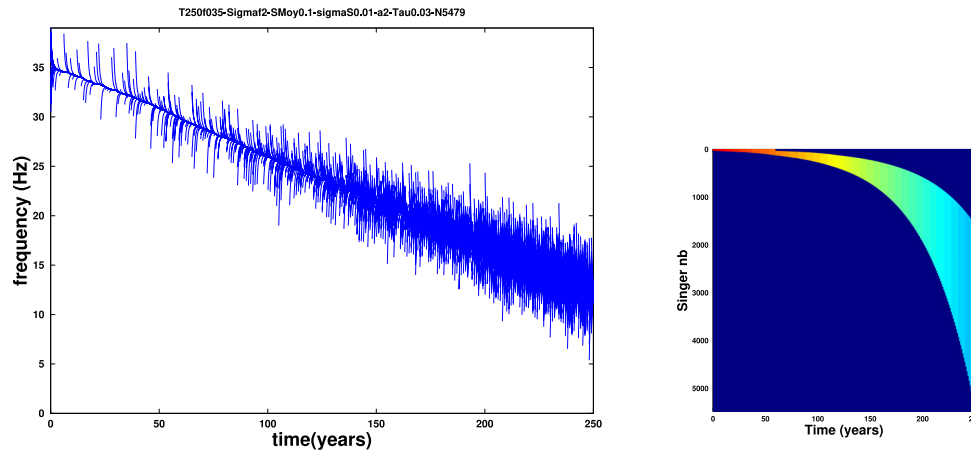


Fig. 3. Simulation of the frequencies of an evolving population. Left: evolution of the frequencies of the 5479 singers of the model, drawing a 'feather' of individual curves converging towards a collective descent. Right: representation of all the frequency vectors, showing the growth of the population with time (in dark blue is a whale that is not participating in the interaction, whether it is not yet 'born' or already 'dead').

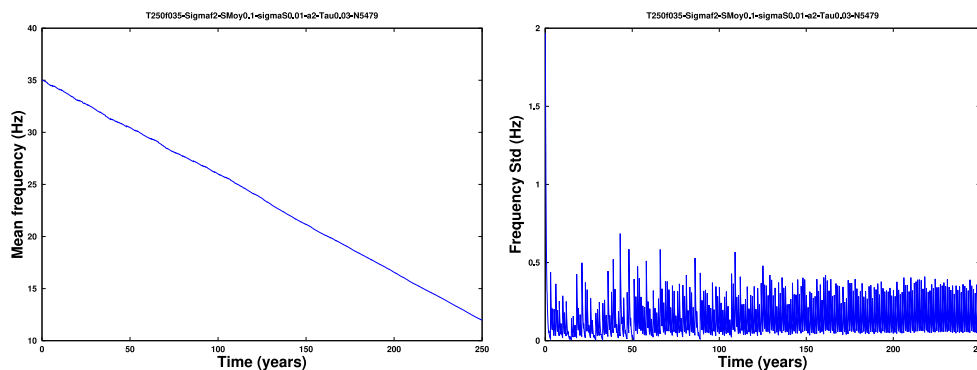


Fig. 4. Evolution of average frequency of the acoustic group (left) and of the standard deviation (right). The average evolution is close to a straight line, the changes in the slope due to the arrival of new singers are not significant.

lower than 0.4 Hz. We thus conclude that the renewal of the population does not affect the global behaviour of the acoustical group.

5. Discussion

5.1. Modelling the linear trend

Our result is mainly qualitative: a simple mathematical model, based on a few biological hypothesis, is able to explain a linear collective behaviour. What's more, this general conclusion is robust to some 'perturbations' in the model due to more complex phenomena, such as complex vocal interactions between agents, or the recruitment of new singers with some diversity of individual starting frequencies. As a result of the robustness of the model (different configurations lead to the same result), however, it does not allow to differentiate between the different configurations. Thus, for instance, the observing of a linear descent does not allow to discriminate between a hierarchical or a symmetric interaction between the whales.

We can make a very rough estimation of the quantitative parameters of our model. These parameters are $F_i(0)$, the initial frequency of each whale (or the frequency at any date t_0 , since the $t = 0$ date is arbitrary), the strength of acoustic influence between the whales a , and ΔF_i for each whale. Given these parameters, our model predicts a global linear descent of slope $V = -a\overline{\Delta F}$ and of average y-intercept $\overline{F_0}$. The dispersion of the frequencies, at a given moment t , is the maximum between $\sigma_{\Delta F}$ and σ_{F_0} (following the

simulation with progressive addition of whales presented in Section 4.3).

Malige et al., 2020 present a review of all published data for each type of song. The slope of the linear descent, expressed in % of the frequency measured in year 2000 per year is generally comprised between 0.3 % per year and 1% per year. If we consider a biologically plausible value for a , so that the convergence time is not very different from 1 year, let's say from one month to 10 years, we derive that the average parameter $\overline{\Delta F}/\overline{F_{2000}}$ is never greater than 10%. This is what we supposed in our biological hypothesis, stating that the whales would tend to sing *slightly* below the general average, which is confirmed by the fact that no individual difference between singers have been observed to the date.

The standard deviation of the frequencies at a given moment is not usually given in the literature. Hoffman et al. (2010) measure $\sigma_F \simeq 0.09$ Hz for B call of the North East Pacific song type ($F_0 \simeq 16$ Hz) and Malige et al. (2020) have an intrinsic dispersion inferior to the quantification error of 0.25 Hz, for the frequency of C and D units of South East Pacific song type 2 ($F_0 \simeq 25$ Hz). We can thus estimate that the relative intrinsic dispersion of the frequencies is usually less than 1% of the frequency. We can conclude from the comparison that the dispersion of the ΔF_i parameters and of the $F_i(0)$ are both lower than 1% of the average frequency of the song, which is coherent with our numerical applications in Section 3.2, Fig. 1 and Section 4.3, Fig. 3. Our model thus seems plausible, given the observed values of the frequency decrease of blue whale songs around the world.

5.2. Individual cultural evolution versus changes in the population

No individual blue whale has been recorded in a timescale sufficient to measure a change in the individual's song. Thus, we could imagine the recorded decrease in frequency to be an *average* property of the group rather than the result of individual coordinated changes. Indeed, a change in post-whaling structure of the population has often been mentioned to explain the change in frequency. In order to quantitatively examine this hypothesis, we computed the two observable variables, namely the slope of the frequency decrease and the dispersion of the data at a given moment, in some simple cases.

First, we consider the case of a progressive modification of the song frequency between generations (possibly under the same advantage of singing lower). This phenomenon is well known in evolution, with a physical character, for instance, being slowly modified to lower the frequency of a reproductive call (Charlton et al., 2013). Let's consider a very simple case of each generation of whales singing δf lower than the whales that appeared the year before, and then maintaining the same song during its life, with a more or less stable population. It is easy to see, then, that the average frequency of the songs of the whole population also decreases of δf per year. On the other hand, the span of song frequencies at a given moment is $(f_{\max} - f_{\min})(t) = T_w \times S$, where T_w is the lifespan of a singing whale ($T_w \simeq 60$ years) and $S = \delta f$ per year, the slope of the linear decrease (see supplementary materials for the detail of the calculation).

Let's consider a different case, where the population of whales is changing due to post-whaling conditions. Let's suppose that the lifespan of the individuals is increasing, and that each individual whale sings lower when it is older. Then, because the lifespan increases, they will be proportionally more and more old individuals and the average frequency will decrease. The computation is slightly more complicated in this case, but we can show that it also leads to $(f_{\max} - f_{\min})(t) > T_w(t) \times S$.

In both cases, then, we find that the span of measured frequencies at one moment is more than 50 times the decrease per year. This is more than an order of magnitude greater than what is found. As shown in Section 5.1, the span of measured frequencies at one moment is estimated to be less than 1 Hz by Hoffman et al. (2010), when the slope of the decrease is 0.15 Hz/year for this population of Northeast Pacific (McDonald et al., 2009). The slopes are different for different parts of the world, but never less than 0.07 Hz/year (case of the unit 3 of the South East Indian song, see McDonald et al., 2009), which would imply, with our calculation, a span of more than 3 Hz, which is not observed. Thus, it does not appear probable that the frequency decrease should be due to a global change in population.

5.3. Modelling intra-annual variations

Seasonal variations in Antarctic blue whales song frequencies have been clearly shown by Leroy et al. (2018), along with some signal of intra-annual variations for other acoustic groups of blue whales in the Indian ocean. This phenomenon is possibly not correlated with the linear decrease. Some hypothesis have been emitted to explain the seasonal variations, such as environmental noise due to ice melting (Leroy et al., 2018), or a variation in the whale density implying a change of frequency through the Lombard effect (Miller et al., 2014), or the change in physiological parameters such as corporeal mass (Miller et al., 2014). Other hypothesis have been discarded, such as a Doppler effect during the migration cycle (Miller et al., 2014). A modification of the sound due to a change in the depth of the animal while singing can also be discarded, since Lewis et al. (2018) show that the depth of a singing whale

can be very different in a single day, while no great dispersion of frequencies have been measured at this scale (Hoffman et al., 2010). What's more, the yearly variations that have been detected could be affected by the differences in the measuring conditions. The number of songs detected varies greatly during the year, as well as the average signal to noise ratio which is much lower in December-January for the Antarctic blue whale songs (Leroy et al., 2018).

On the whole, the great diversity of parameters varying in a yearly basis makes it difficult to find one single explanatory phenomenon. Whatever the cause, we have shown in Section 4.2 that forcing a seasonal change in the ΔF_i parameters implies a seasonal variation in the resulting average frequencies. As an example, we have modelled the intra and inter annual variations of the Antarctic blue whales found by Leroy et al. (2018). For this example we supposed that, for each whale i , $\Delta F_i(t) = \Delta F_{i(a)} + \Delta F_{i(b)} \cos(2\pi t/T + \phi)$ where $\Delta F_{i(a)}$ and $\Delta F_{i(b)}$ are constant characteristics of the whale i , T is equal to one year, and ϕ is a constant phase difference for all the whales. The details of the computation are explained in the supplementary materials.

Fig. 5 shows that our model can easily incorporate some yearly influence over the whale songs. As an explanation that is consistent with our first hypothesis, we can propose a mechanism for the yearly variation of the frequency. The frequency variations corrected from the general linear decrease, as measured by Miller et al. (2014) or Leroy et al. (2018) for the antarctic blue whale, show a general increase between October and April and a decrease afterwards. These variations can be interpreted in the mark of the yearly reproduction-feeding cycle of the antarctic blue whales (Mizroch et al., 1984; Sears and Perrin, 2018). During austral summer, a feeding period, less songs are detected and the pressure of reproduction seems lower. We could imagine that, in this context, the need to sing lower than the other whales (ΔF_i) could be less and even have negative values, whereas during the austral autumn and winter, which are probably seasons for the reproduction, the competition is higher and ΔF_i is greater in average.

5.4. Isolated whales

An interesting case for our model is the case of isolated whales. Indeed, the discovery of a group of whales, acoustically isolated from their original group, which would still follow the same trend as the group from which it has been separated would be a unique way of disproving our hypothesis. Rojas et al. (2022) recently published the case of a song belonging to the acoustical group of the South East Pacific (SEP2) recorded in the Atlantic Ocean, near South Georgia by Pangerc (2010), far from its normal location. The data is compatible with one vagrant individual, no superimposition of songs having been recorded, though it could also be due to a (small) group of whales. A blue whale emitting the South East Pacific song type (SEP song type) near South Georgia can be considered acoustically isolated from the known population of blue whales emitting the same song type. Indeed, South Georgia is at more than 1500 km from Cape Horn and the group emitting SEP songs is located between Chiloe Island and Galapagos, far more at the north, on the Pacific side of South America (see Malige et al., 2020 for a review of the available recordings).

When compared to the measured trend for this type of song, we find that the recordings from South Georgia does not fit the linear descend of its acoustical group of origin (see Fig. 6). This very interesting case could be interpreted in the mark of our model as a vagrant whale (or a small group of whales) that, being acoustically separated from its acoustical group for several years, has evolved differently. Our model would then predict that the separation occurred around the year 2001 or before, depending on the evolu-

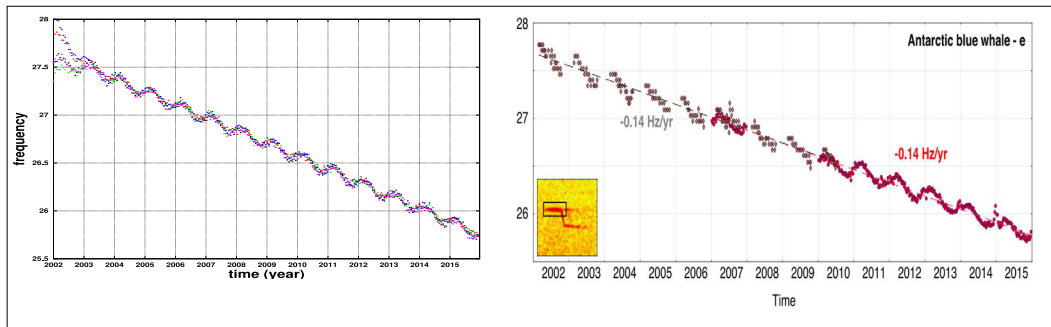


Fig. 5. Left: result of the modelling of the frequency variations of the unit A of the Antarctic blue whales song. Parameters of the model: $n = 10$ whales (of which only 5 are represented for clarity), initial average frequency $\bar{F}_0 = 27.7$ Hz, with a standard deviation of $\sigma_{F_0} = 0.08$ Hz, $\Delta\bar{F}_{(a)} = 0.076$ Hz, $\sigma_{\Delta F_{(a)}} = 0.01$ Hz, $\Delta\bar{F}_{(b)} = 0.22$ Hz, $\sigma_{\Delta F_{(b)}} = 0.05$ Hz, $a = 1.825 \text{ yr}^{-1}$ and $\phi = 2.9$ radians. A random noise has been added to the data, with a zero average and a 0.02 Hz standard deviation. Right: data of the frequency variation obtained by Leroy et al. (2018).

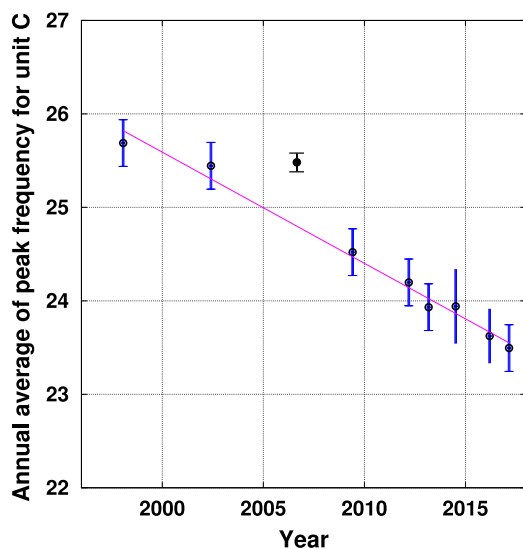


Fig. 6. Linear decrease for peak frequency of unit C of the South East Pacific song SEP2, from Malige et al. (2020). The measure in 2006 is a recording of an isolated whale (or group of whales) in South Georgia: it is significantly out of the general evolution of the song. Figure taken from Rojas et al. (2022).

tion of the isolated song which is unknown, since we only have one period of recording (during about 15 days).

5.5. Long term evolution

A linear decrease in frequency obviously cannot last for ever. For instance, if prolonging the trend, unit B of the song of the North East Pacific, as well as unit A of the song of the North West Pacific, would reach a 0-frequency in less than a century. Thus, some change in the evolution of the songs is bound to appear. A possibility, that could be termed 'revolution' by analogy of the studies on Humpback whales songs (Allen et al., 2018), is a rapid change in frequency bringing back the song to a higher frequency level. A possible example of such a 'revolution' could be the case of the so-called "spot call" presented by Ward et al. (2017). This call, recorded from 2002 in South Australia, has not been attributed yet with security to a specific species, but it is strongly suspected to be from a great whale. During the years 2006–2007, its measured frequency stopped its linear evolution with a jump from 23 Hz to 28 Hz, again followed by a linear decrease (of about 1% of 2007 value per year) on the following years. Although this call is more probably due to a right whale (*Eubalaena australis*) than a blue

whale (Ward et al., 2017; Leroy et al., 2017), it might be a clue to understand the future of blue whales songs, and clearly advocates for a cultural process.

Alternatively, the observed linear trend of frequency decrease could be an approximation of a slow exponential decrease. Calculus show that, for the longest studied song (the North East Pacific song type), the global trend differs from an decreasing exponential of not more than a few percent, more or less the level of precision of the measurements. In a recent study, Rice and colleagues show that for the North East Pacific song type, the long term decrease is not strictly linear (Rice et al., 2022) and an exponential model would perhaps better fit the data. This point is interesting because in a few years, it will probably be possible to differentiate a linear from an exponential decrease for many song types, since the difference between the two functions obviously grows with the length of observation. We tried a slightly different hypothesis for our model, supposing each whale to be singing at a frequency given by a certain percentage of the average frequency, leading to the following equation:

$$\frac{d}{dt} F_i(t) = -a(F_i(t) - \alpha \bar{F}(t)) \tag{12}$$

where α is a coefficient lower than (but close to) 1. It is easy to see that in this case, the average frequency will follow an exponential decrease. What's more, the individual frequencies will still converge to a common exponential behaviour (see supplementary materials). Actual data is not precise enough to actually decide between a strictly linear decrease or a slow exponential decrease. However, a few more years of observation could lead to exiting new data for the long term evolution of blue whale songs.

6. Conclusion

The role of culture in cetacean societies has been much investigated since (Rendell and Whitehead, 2001; Whitehead and Rendell, 2015) important reviews. In such complex evolution as the Humpback whale song, it has been widely acknowledged (Garland and Mcgregor, 2020). For the much simpler evolution of the blue whale songs, however, ecological influence cannot be so easily ruled out, and thus it has been cited as a possible reason for the frequency decrease observed (McDonald et al., 2009).

Cultural transmission has not been studied in detail for this species. Here, we tried the plausibility of a cultural simple phenomenon to explain the linear frequency decrease of blue whales songs worldwide. From the hypothesis that the males are submitted both to a conformity pressure and to a reproductive advantage of singing lower than the other males, we constructed an agent-

based model to explore the frequency evolution resulting from it. Our model predicts in a robust way a linear frequency decrease compatible with published data.

To have a chance to disprove our hypothesis, it would be interesting to follow up groups of whales acoustically separated from their original group. We consider that the actual context of recolonization of the populations of blue whales (Branch, 2008) is favourable to the apparition of vagrant whales or groups of whales re-colonizing old territories, making such observations possible. On the other hand, long term follow up of known acoustical groups are fundamental, while we expect that some change in the frequency decrease is bound to appear at a decadal timescale, since the frequency cannot decrease linearly for ever.

Additionally, frequency decrease are possibly present for other species, such as fin whales (*Balaenoptera physalus*) and bowhead whales (*Balaena mysticetus*), thought it is not as easy to measure as for blue whales who are characterized by their very uniform and tonal songs (Thode et al., 2017; Weirathmueller et al., 2017; Leroy et al., 2018). Thode et al. (2017) shows that the average frequency decrease of the bowhead calls cannot be explained by individual size variation trends or density of population. The long-term frequency analysis of a potential baleen whale call shows also that a more complex evolution, combining decadal frequency decrease and increase, can happen (Pinto and Chandrayadula, 2021). It is plausible that these other species may show the same cultural mechanisms as blue whales, though modulated for each species.

Finally, further studies of the evolution of blue whales songs could be focused on the apparition of the local calls or 'dialects'. Following Lemon (1966), three factors are necessary for the apparition of different dialects in a species: some geographic isolation, a cultural transmission between generations and some source of diversity inside the vocalization. In the case of blue whales, these conditions are fulfilled, and the frequency decrease could be one source of diversity inside the song, since all units do not decrease with the same rate inside one specific song. According to our modelling, if one acoustic group is culturally divided, the two resulting groups will evolve differently, possibly giving birth to two different dialects.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jtbi.2022.111184>.

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