

An individual-based model to infer the impact of whalewatching on cetacean population dynamics

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Abstract

Whalewatching play an important socioeconomic role in many countries. Yet after 20 years of research in its effects on the targeted populations, its sustainability is now questioned. While much progress has been made to understand the short-term influences of boat-cetacean interactions for individuals and schools, the long-term consequences of those remain uncertain. Recent studies showed that the stress related to both interactions themselves and the avoidance strategies individuals used can affect the fitness of individuals and their reproductive success. The decrease in individual fitness can itself result in lowered survival probabilities, because of increases in either mortality or emigration rates. We introduce an individual-based model of population dynamics which attempt to incorporate these findings to understand their potential consequences for the dynamics of populations. This model is based on realistic scenarios in which schools of individuals are exposed to boat interactions on a daily basis. This results in different yearly cumulative exposure to boat for each individual. The relationship between survival and reproductive parameters are then linked for each individual to their boat exposure using logistic functions. Variance is introduced in these functions to highlight both the uncertainty in the relationships as well as individual variation in effect size. Using two case studies we show that whalewatching can influence the dynamics of cetacean populations and can also jeopardise the viability of populations which are already at risk.

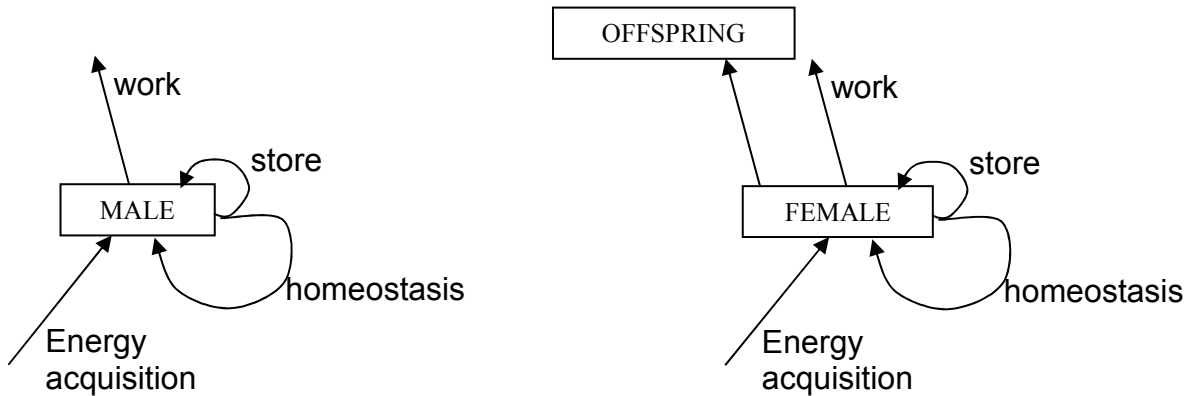
Introduction

Whalewatching plays a crucial role in increasing the public awareness about the plight of the oceans (Hoyt 2001). It is often quoted as a life changing experience by participants and help raising the awareness about conservation issues relating to cetaceans in particular (Forestell 1993). For this, these activities play a key political role in the conservation of marine mammals around the world and the protection of their habitat. In addition, whalewatching revenues are locally important and in some areas economically important at the national level (Hoyt 2001). Whalewatching can therefore be perceived as a good alternative to enhance the ecological and economical sustainability of coastal communities. Whalewatching is a non-consumptive activity and therefore was first perceived as having no potential to alter the resources on which it was based. However, after 20 years of research we are now realising that whalewatching can indeed impact the targeted cetacean populations in various ways notably by altering their energetic budgets, displacing them from their habitats, and altering their population biology parameters (Bejder 2005; Bejder et al. 2006a; Bejder et al. 2006b; Constantine et al. 2004; Lusseau 2004; Lusseau 2003; Lusseau 2005a; Williams et al. 2002). Whalewatching, like most other human activities, can therefore act as an evolutionary selection force, altering the life of the targeted population (Bejder 2005; Bejder et al. 2006b). Currently we have little understanding about the long-term implications of these impacts. Here we offer a model framework in which the implications of these effects can be explored. This model attempts to integrate the information we currently have on the impact of whalewatching on individual, or school of, cetaceans in a population dynamics model. The model we present was left as general as possible to highlight its applicability to many species and location. Therefore the results we present are limited but highlight the information that needs to be acquired to better understand the relationship between short-term impacts and long-term consequences at the population level.

Rationale: energetic budget of individuals

The model is based on an energetic representation of individuals (Figure 1). From studies of whalewatching impacts it seems that individuals will have to either work more (for example travel more) or forgo foraging when interacting with boats. In most instances the relationships between these impacts and the survival probability of individuals is unknown. However, in some cases this relationship can be inferred from observed behaviour such as habitat displacement, seen as fitness decisions for the individuals (Bejder et al. 2006b; Lusseau 2005a). From this and understanding of physiological constraints on individuals we assumed a logistic relationship between boat exposure and survival probability. Recent work (Bejder 2005) has demonstrated such a response function between boat exposure and reproductive success in female bottlenose dolphins for which energetic mechanisms explaining this relationship had been hypothesised (Lusseau 2003).

(a) CONTROL:



(b) DIRECT OBSERVED IMPACT:

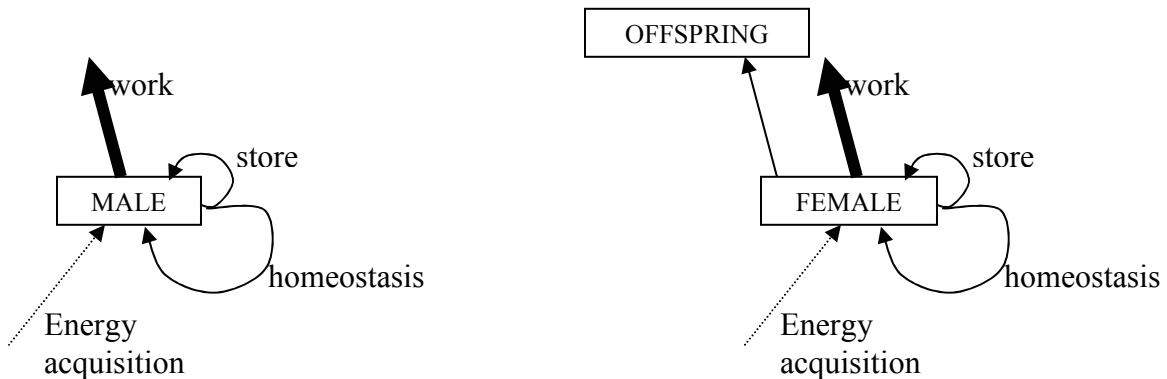


Figure 1. Conceptual framework representing individuals as energy processing systems (a), direct observed impacts of whalewatching are identified as increase in work load or a decrease in energy acquisition (b).

Studies of stress in mammals (Moberg and Mench 2000), as well as work on life history theory (Metz et al. 1992; Promislow and Harvey 1991), show that these assumptions are reasonable. Following the first law of thermodynamics, any alteration to the interactions between the individual and its environment (work and energy acquisition) must be balanced by alterations in its internal states, and in the case of females by alterations in the calf-female energetic relationships (mother-calf can be regarded as a semi-closed system before weaning). Little is known about the plasticity of dolphin and whale homeostasis and its interactions with stored energy. However, in other mammals females tend to prioritise internal energy balance to outputs to offspring, resulting in lower reproductive success in stressful situations. In domestic mammals decreased energy intake typically causes delayed sexual maturity and longer breeding intervals in

adults by suppressing ovulation and oestrous behaviour (Allen and Lamming 1961; Booth 1990; Ducker et al. 1982). An increase in energy expenditure can have similar effects if not matched by an increased energy intake (Cameron et al. 1990). These mechanisms prevent the female from both engaging in and wasting energy in a pregnancy that is likely to be unsuccessful.

The consequences of nutritional stress caused either by decreased foraging success or unmatched increased energy expenditure leads to lower birth weight in the offspring (LeBoeuf and Crocker 2005) or loss of fetus (Moberg and Mench 2000). The most dramatic effects of nutritional stress on the mother is not during pregnancy however, but during lactation which is in general much more energetically demanding to the female than the pregnancy (Wade and Schneider 1992) Weaning weight is lower in offspring of mothers with restricted food intake during lactation and as a consequence has lower survival rates.

An individual-based model

Individual based models (IBM) are quickly becoming an important tool in ecology to capture the heterogeneity in the life history of individuals (Grimm and Railsback 2005). They are especially useful in understanding the emerging consequences of the interactions of non-linear influences on individuals for the dynamics of populations. Here we used an IBM approach to understand how often individuals in a population are exposed to boat interactions. We then related these measures of exposure to life parameters known to be possibly affected by those interactions using logistic functions.

Each year a number of individuals were exposed to boat interactions in the following manner. Every day N interactions are triggered with their duration being taken from a gamma function with a parameterised average t and standard deviation t_sd . In addition the time elapsed since the last interaction was also selected from a gamma distribution parameterised using realistic values. For each interaction n dolphins are randomly selected, n is chosen from a gamma function with a parameterised average and standard deviation which mimics the frequency distribution of school size in the population. For these selected individuals cumulative boat exposure, number of interactions to which they have been exposed and the average time elapsed between two interactions to which they were exposed was updated.

Individuals died and reproduced at the end of the year and their boat exposure parameters were reset at the end of each year. The basal survival and reproductive rates of individuals is estimated from measured population parameters, and for many populations it is possible to define age-sex class-specific rates.

The model was run 100 times for 100 years and trends in population size were measured for each model run.

Relating survival and reproduction rates to boat exposure

From recent work it appears that survival rate can be affected by the time that elapses on average between two interactions (Lusseau 2004). Reproduction rate seem to be affected by the cumulative amount of time a female was exposed to boats.

We used logistic functions informed by four parameters to model the relationship between these two population parameters and the boat interactions parameters (Figure

2). The four parameters provide information about the maximum rate the population parameter can take (given rate without boat exposure), the breadth of effects, the inflection point at which the transition occurs and the steepness of the slope during the transition.

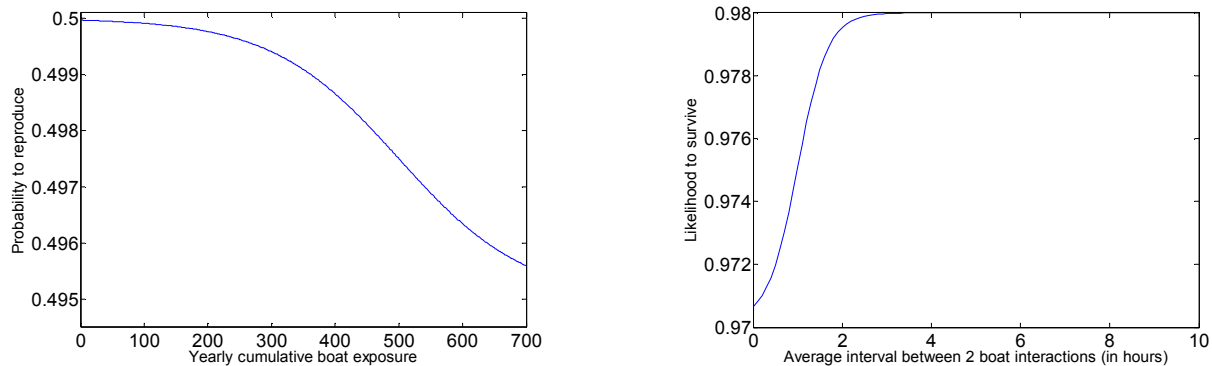


Figure 2. Logistic function representing the relationship between boat exposure and reproduction rate (a) and between the average time elapsed between two boat interactions and likelihood to survive. The effect size in both figures is small (1%), in figure 2a the effect is not as pronounced as in figure 2b (the phase transition is not as sharp).

Variance in the information about the logistic functions

We introduce variance in the knowledge we have about the way survival and reproduction rates are influenced by boat exposure. Instead of one known inflection point for each function we used a value selected randomly from a uniform distribution with lower and upper bounds representing the range within which one could assume exposure to influence those rates. Similarly, we can also introduce variance in the effect of boat exposure. Both these error terms were introduced in two separate different ways. First the values were randomly drawn for each model run, and then the values were randomly drawn for each individual at each boat interaction.

Implementation

The model code was implemented in Matlab on both Windows and Linux platforms. Models were run concurrently on a 16 nodes computer cluster (Linux environment) at the Mathematics and Statistics department in Dalhousie University (Appendix 1). The largest model (2700 individuals with 16 interactions per day) took 12 hours to run on the cluster.

Example 1: A small population: Doubtful Sound, New Zealand

Based on known population biology parameters for this population (Haase and Schneider 2001) we initialised the model using the following rules. Individuals aged 1 to

4 are calves and have a lower survival rate (Haase 2000; Haase and Schneider 2001). Females start reproducing at age 12 and passed age 30 individuals have a lower survival rate and reproductive rate. Once females have calves they do not reproduce for another 4 years. If a mother dies and her calf is less than 4 years old it dies as well. The sex of calf was randomly assigned (50/50 chance). Population size at year 1 was 62 (Williams et al. 1993).

Previous studies provided information on the characteristics of boat-dolphin interactions in this fjord. Typically there were 16 interactions per day, over the whole population, lasting 0.18 hours on average (Lusseau 2005b). We assumed uninformed effects on survival and reproductive rates which were randomly assigned between 0 and 5%.

It is interesting to see that even with such low effect size (an order of magnitude lower than the ones observed in Shark Bay), the population is likely to go extinct within 30 years (Figures 3-5). More interestingly, the relationship between the number of interactions/day and abundance trends is not linear, with likelihoods of a decrease remaining similar when the number of interactions is halved, but the magnitude of the decrease being accentuated by the number of boat interactions.

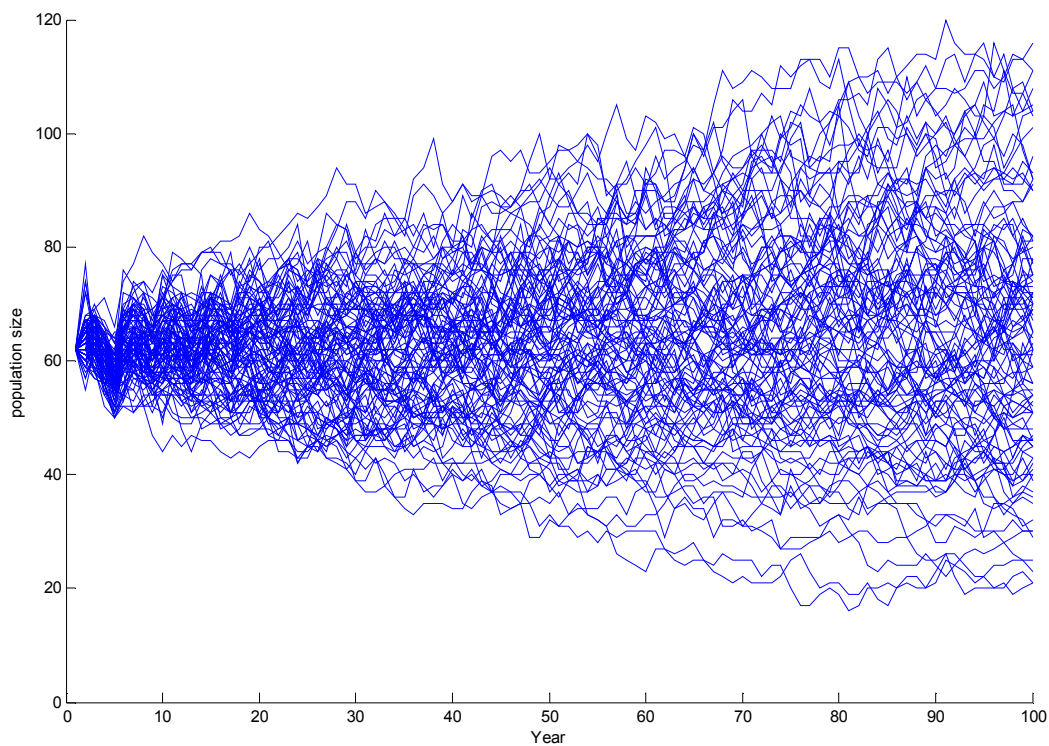


Figure 3. Population dynamics model for Doubtful Sound without any interactions. The population never goes extinct and abundance estimates range from 18 to 118 after 100 years, encompassing the current known abundance. The likelihood population abundance will decrease by 10% is 0.38, the likelihood population abundance will half is 0.07, and the likelihood the population will go extinct is 0.

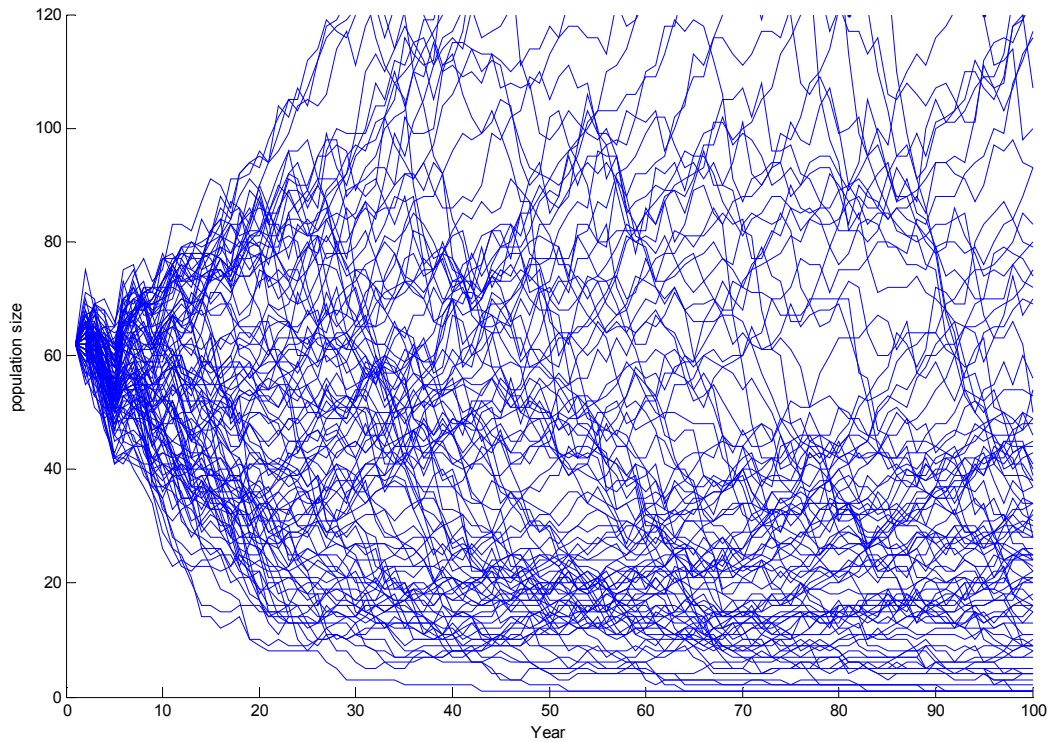


Figure 4. Models ran with a 0 to 5% effect size on both the reproductive and survival rates and 7 interactions per day. The inflection points changed for each run and the effect size is randomly selected for each individual and for each year. Population abundance ranges from 0 to 350 after 100 years. The likelihood population abundance will decrease by 10% is 0.74, the likelihood population abundance will half is 0.31, and the likelihood the population will go extinct is 0.13. Extinction may occur within 30 years.

The fate of the population also becomes more stochastic with the range of possible population size after 100 years increasing drastically once boat interactions are introduced. This is most likely due to the lack of density-dependence effects on population parameters. Introducing those and allee effects (Stephens and Sutherland 1999) would increase the precision of outcomes. These latter effects would also accentuate the decline in the population because it is small.

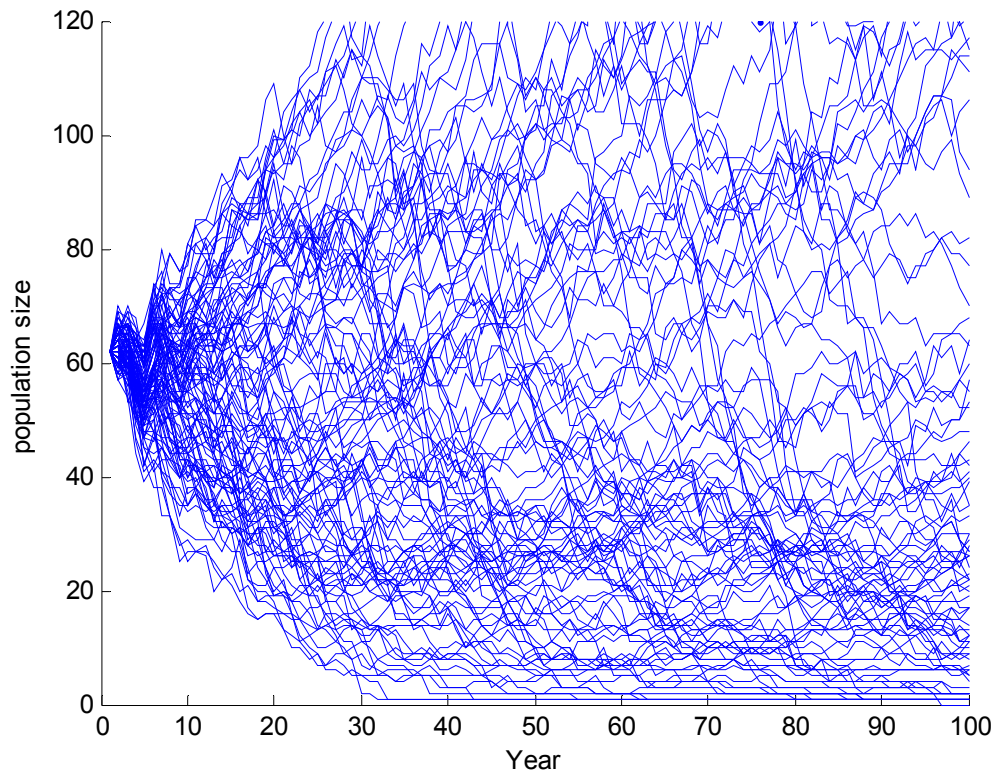


Figure 5. Models ran with a 0 to 5% effect size on both the reproductive and survival rates and 16 interactions per day. The inflection points changed for each run and the effect size is randomly selected for each individual and for each year. Population abundance ranges from 0 to 350 after 100 years. The likelihood population abundance will decrease by 10% is 0.69, the likelihood population abundance will half is 0.56, and the likelihood the population will go extinct is 0.19. Extinction may occur within 30 years.

Example 2: A large population: Shark Bay, Australia

We subjected a larger population, similar to the Shark Bay bottlenose dolphin population, to the same boat exposure (Figures 6-8). Population size (2700 at year 1) and population biology parameters were drawn from published data (Mann et al. 2000). Individuals were also drawn randomly from the whole population to be exposed to boats, which is different from the real situation in Shark Bay where only a small subset of the population (~120) is exposed to boat interactions (Bejder 2005).

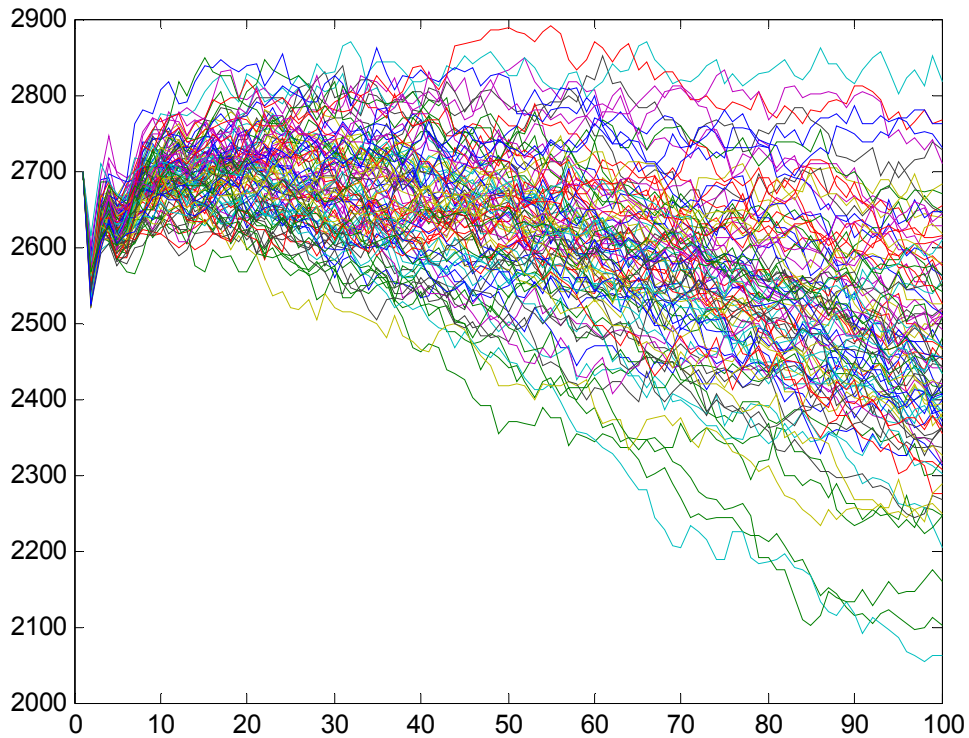


Figure 6. Population dynamics model for Shark Bay without any interactions. The population never goes extinct and abundance estimates range from 2062 to 2816 after 100 years, encompassing the current known abundance. The likelihood population abundance will decrease by 10% is 0.43, the likelihood population abundance will half is 0, and the likelihood the population will go extinct is 0.

While boat exposure does not have as drastic an effect as in Doubtful Sound, it is still clear that the intensity of boat exposure does not have a linear effect on population viability. The population exposed to 7 interactions is not likely to differ from the population unexposed to boats; however once the population is exposed to 16 interactions, it is likely to decrease by half over 100 years and there is even a small chance that it will go extinct. This non-linear effect highlights that whalewatching can drive a population in an extinction vortex (Gilpin and Soule 1986) if whalewatching effort remains constant as the population declines.

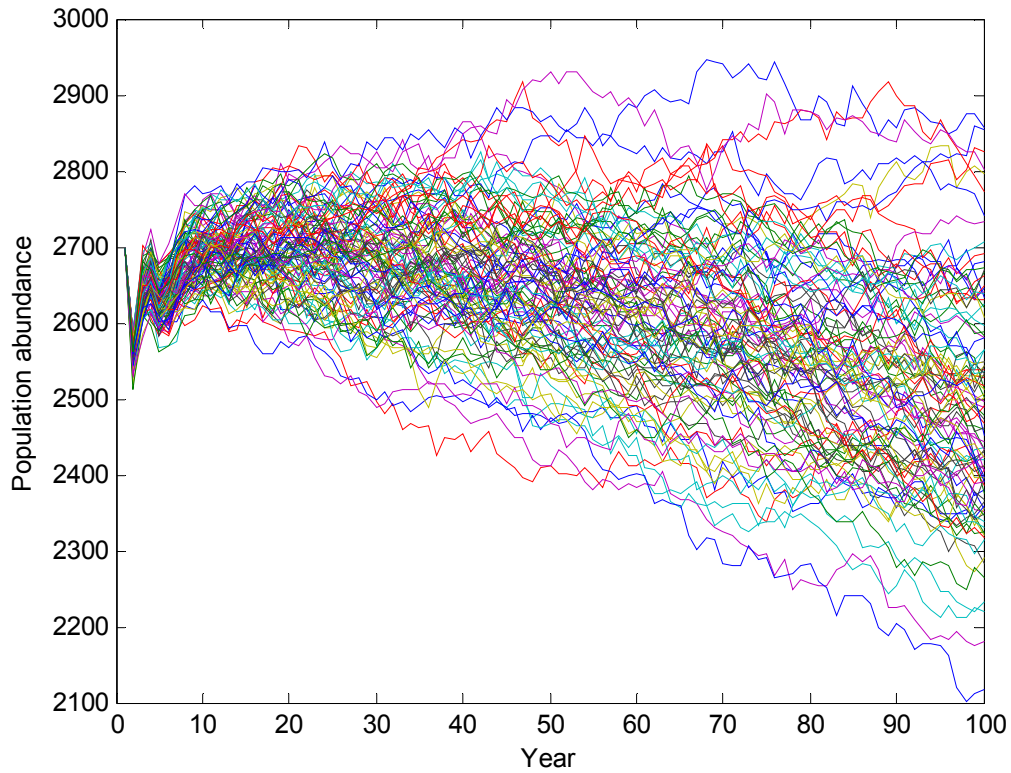


Figure 7. Models ran with a 0 to 5% effect size on both the reproductive and survival rates and 7 interactions per day. The inflection points changed for each run and the effect size is randomly selected for each individual and for each year. The likelihood population abundance will decrease by 10% is 0.38, the likelihood population abundance will half is 0, and the likelihood the population will go extinct is 0.

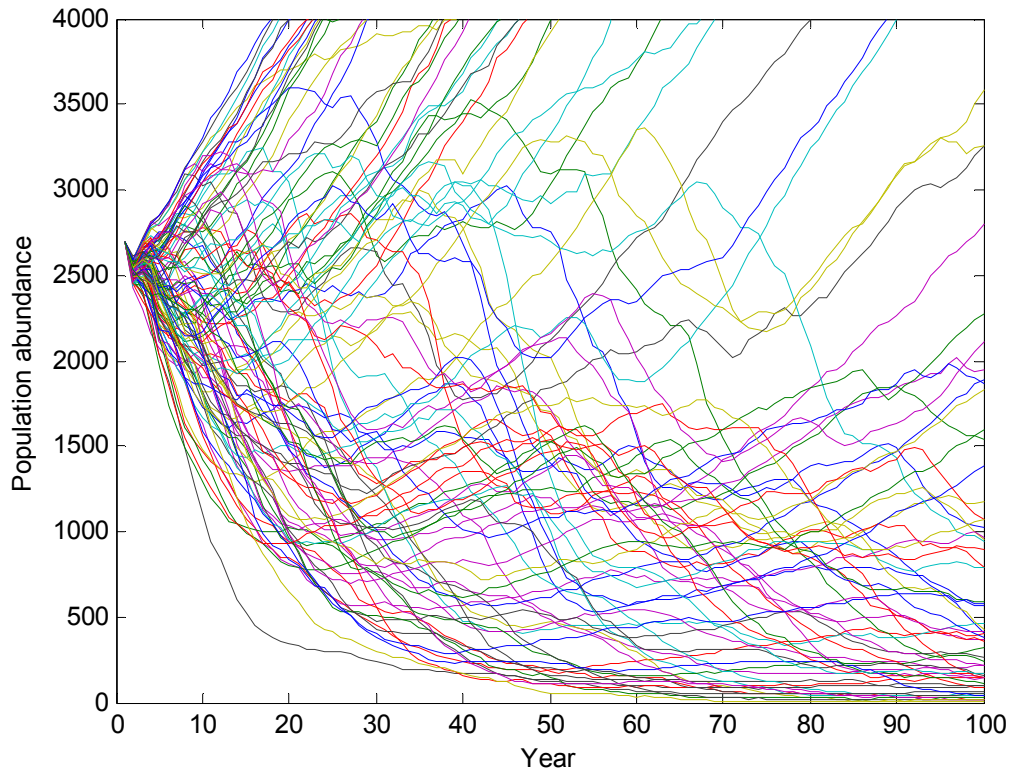


Figure 8. Models ran with a 0 to 5% effect size on both the reproductive and survival rates and 16 interactions per day. The inflection points changed for each run and the effect size is randomly selected for each individual and for each year. The likelihood population abundance will decrease by 10% is 0.58, the likelihood population abundance will half is 0.49, and the likelihood the population will go extinct is 0.01.

Discussion

This individual based model is versatile. It provides a basis from which more complicated relationships can be assessed. For example, one can include a stochastic component, such as disease with varying susceptibility for individuals, and assess the interaction between this factor and whalewatching. Since this framework is hierarchical in its nature more complex relationships can be added on such as the effects of the length of interactions, or the behaviour of boats during interactions. Similarly the influence of uncertainty relating to the relationships between boat exposure and whalewatching can be incorporated by randomising these components of the model.

At the stage the link between boat exposure and individual fitness is only related through survival rate and reproduction rate. More complex relationships can be applied once more information about the physiological ecology of cetaceans become available. Much research effort is needed to understand how cetacean species utilise their energy store, integrate challenges to homeostasis through time, and prioritise energy expenditure. The influence of cetacean sociality can also be assessed by incorporating this information in the composition and size of the schools selected to be exposed to boat interactions (at this stage individuals are picked at random from the population).

This model does not currently account for other factors that may be affecting the relationship between boat exposure and survival probability such as immunosuppression due to chronic or acute stress exposure or other physiological damages incurred from boat exposure, such as decompression sickness or death caused by boat strikes (Lusseau et al. 2002) for example. From studies on life history strategy in mammals and birds we know that immune response can also be linked to individual's fitness. Therefore immunity of individuals can be incorporated as a factor as soon as more information is available for these species and its influence on population viability can be tested by challenging the population with stochastic disease events. Currently this is a discrete model, individuals breed and die at the end of each year and also the exposure rate is reset at the beginning of each year. Future development will have to move this model in a continuous time frame. This IBM can also easily be fitted in an ecological-socioeconomic model, balancing economic viability with population viability (Casagrandi and Rinaldi 2002).

Extinction vortex and selection pressure

Once populations start to decline, the pressure of whalewatching on the remaining individuals increases because the whalewatching effort remains constant. This in turn accentuates the whalewatching contributions to the population decline and the system becomes entangled in an extinction vortex. However, introducing variation in the effect of whalewatching on individuals (in our case by randomly drawing effect size for each individual and each year between 0 and 5%) help maintaining the outcome of each scenario more chaotic (Figures 4 and 5) highlighting a R-type vortex- decrease in N , and increase in variance- (Gilpin and Soule 1986). Applied to realistic scenario, this effect would translate in the elimination of sensitive individuals from the populations either through mortality or emigration (as observed by Bejder 2006b). Whalewatching has therefore the capacity to act as an evolutionary pressure on these populations, which may jeopardise their long-term viability. Human-induced evolutionary pressures tend indeed to be maladaptive as observed in cod (Olsen et al. 2004) and bighorn sheep (Coltman et al. 2003).

We do not know how realistic this scenario may be since the economic viability of whalewatching operations will be linked on the likelihood to encounter individuals which will require an increased search effort when the population declines. Therefore population decline may be followed, in a non-linear, lagged fashion, by a decreased whalewatching pressure. This issue needs to be investigated further by integrating this ecological model in a socio-economic model of whalewatching.

Some guidance

When applying this model to cetacean populations it is important to be aware that the currently measured reproductive and survival rates may already be affected by whalewatching if this industry is pre-existing. If they are available pre-whalewatching measures should be used and if not use measures could be inferred from other populations. If none exist, test the sensitivity and robustness of the model to these rates.

Conclusions

Since whalewatching activities can impact the energetic budget of cetaceans, it has the possibility to impact the dynamics of these populations as well as introduce new evolutionary selection pressures. Despite its simplicity, we can already draw important conclusions from this individual-based model. It is important to note that once whalewatching can reduce the survival probability of individuals its influence on the population is going to be accentuated as population size declines and whalewatching pressure remain constant. The cetacean population-whalewatching system can rapidly drop in an extinction vortex.

We feel that this question needs to be urgently addressed more in-depth, therefore we are making the Matlab code of this model available as an appendix. It will also be freely downloadable at <http://www.lusseau.org>. We will compile contributions made to the model (either by us or by others) and make them immediately available on this website. We hope that this will encourage others to both apply this IBM approach to specific case studies and increase the complexity of the model by incorporating more complex variables such as boat behaviour, sociality, or species-specific physiological constraints effects.

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c=c0;
am1=am10;
am2=am20;
af1=af10;
af2=af20;
pop_size=c+am1+am2+af1+af2;
low_r_effect=200;%set the lower bound at which reproduction rate may be affected
up_r_effect=400;%set the upper bound at which reproduction rate may be affected
low_s_effect=1;%set the lower bound at which survival rate may be affected
up_s_effect=1.3;%set the upper bound at which survival rate may be affected
pop=zeros(11,pop_size);

%randomly initialise the age of each individual in the population according
%to their age class
pop(6,1:c)=unidrnd(age_maturity,1,c);
pop(6,c+1:c+am1)=age_maturity+unidrnd(age_threshold-age_maturity,1,am1);
pop(6,c+am1+1:c+am1+am2)=age_threshold+unidrnd(50-age_threshold,1,am2);
pop(6,c+am1+am2+1:c+am1+am2+af1)=age_maturity+unidrnd(age_threshold-age_maturity,1,af1);
pop(6,c+am1+am2+af1+1:c+am1+am2+af1+af2)=age_threshold+unidrnd(50-age_threshold,1,af2);

%populate the population array
%first row is id, second is sex, third is age, fourth is pb (initialised),
%and fifth is tb (initialised), sixth row is the age of the animal, 7th is
%survival rate, 8th reproductive rate, and 9th is the mum tracker (values
%ranging from 1 to 4 for mums preventing them to have a calf while they are
%already caring for another
pop(1,1:pop_size)=1:1:pop_size;
pop(2,1:c)=1;
pop(3,1:c)=1;
pop(2,c+1:c+am1+am2)=2;
pop(2,c+am1+am2+1:c+am1+am2+af1+af2)=3;
pop(3,c+1:c+am1)=2;
pop(3,c+am1+1:c+am1+am2)=3;
pop(3,c+am1+am2+1:c+am1+am2+af1)=2;
pop(3,c+am1+am2+af1+1:c+am1+am2+af1+af2)=3;
pop(4,1:pop_size)=0; %number of interactions
pop(5,1:pop_size)=0; %boat duration exposure
pop(7,1:c)=sc; %survival rate
pop(7,c+1:c+am1)=s1;
pop(7,c+am1+1:c+am1+am2)=s2;
pop(7,c+am1+am2+1:c+am1+am2+af1)=s1;
pop(7,c+am1+am2+af1+1:c+am1+am2+af1+af2)=s2;
pop(8,c+am1+am2+1:c+am1+am2+af1)=r1; %reproductive rate
pop(8,c+am1+am2+af1+1:c+am1+am2+af1+af2)=r2;
pop(9,1:pop_size)=0; % mum tracker
pop(10,1:pop_size)=0; %mum calf pairing
pop(11,1:pop_size)=0; %inter-boat interaction interval

a=1; % this tracks mum-calf pairs
for year=1:Y
    pop_size=c+am1+am2+af1+af2;
    population(year)=pop_size;
    adultfemale(year)=af1;
    oldfemale(year)=af2;
    calf(year)=c;

    %%%EXPOSURE%%
    for day=1:365
        for interaction=1:N_boat
            t=gamrnd(t_boat^2/t_sd_boat^2,t_sd_boat^2/t_boat); %gamma distribution length of interaction
            ibi=gamrnd(ibi_boat^2/ibi_sd_boat^2,ibi_sd_boat^2/ibi_boat); %gamma distribution time since last interaction
            %randomly pick without replacement n individuals and assign their pb
            %and tb with new values
            school=round(gamrnd(n_school^2/sd_school^2,sd_school^2/n_school));%gamma distribution
            R=randsample(pop(1,:),min(school,pop_size));
            %no adaptive response of school size to population size that can be arranged using another
            %function which adjust school size and stdev to maintain the same ratio
            %between school size and pop size at each year as between the original

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    %data
    pop(4,R)=pop(4,R)+1;
    pop(5,R)=pop(5,R)+t;
    pop(11,R)=pop(11,R)+ibi;

end

end
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%ALTER BIOLOGICAL PARAMETERS%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%survival probabilities are logistic functions with max being calculated survival probability
%(<1) and decreasing with boat variables
% using 4-parameter logistic functions:
% f(x)= a + (b/(1+exp(c*(x-d))))
% a is the lower bound of the curve
% b is the breadth of the curve (upper-lower bounds)
% c is a parameter informing the steepness of the slope
% d is the inflection point
if pop(5,:)~=0
    pop(7,:)= (pop(7,:)-(0 + (psr-0).*rand(1,1))*pop(7,:)) + (((0 + (psr-0).*rand(1,1))*pop(7,:))/(1+exp(-3*((pop(11,:)/pop(4,:))-
(low_s_effect + (up_s_effect-low_s_effect).*rand(1,1)))))); %survival is affected by average time left between boat encounters
    pop(8,:)= (pop(8,:)-(0 + (pr-0).*rand(1,1))*pop(8,:)) + (((0 + (pr-0).*rand(1,1))*pop(8,:))/(1+exp(.01*((pop(5,:))-
(low_r_effect+unidrnd((up_r_effect-low_r_effect),1)))))); %reproduction rate is affected by boat exposure
end
%assign who survives
d=1;
while d<pop_size
    rd=rand(1,pop_size);
    if pop(7,d)<rd(1,d)
        place_holder=pop(10,d);
        pop(:,d)=[];
        kill=find((pop(10,:)==place_holder)&(pop(6,:)<5)); %kills the calf of mums that die (if calf <4 years old)
        if size(kill,1)~=0
            pop(:,kill)=[];
        end
    else
        d=d+1;
    end
    pop_size=size(pop,2);
end

%assign who gives birth

d=1;
while d<pop_size
    rd=rand(1,pop_size);
    if (pop(2,d)==3)&(pop(3,d)==2)&(pop(9,d)==0)&(pop(6,d)>12)&(rd(1,d)<pop(8,d))
        pop(1,pop_size+1)=pop_size+1;
        pop(2,pop_size+1)=1;
        pop(3,pop_size+1)=1;
        pop(4,pop_size+1)=0;
        pop(5,pop_size+1)=0;
        pop(6,pop_size+1)=1;
        pop(7,pop_size+1)=sc;
        pop(8,pop_size+1)=0;
        pop(10,pop_size+1)=a;
        pop(9,d)=1;
        pop(10,d)=a;
        a=a+1;
    else
        if (pop(2,d)==3)&(pop(3,d)==3)&(pop(9,d)==0)&(rd(1,d)<pop(8,d))
            pop(1,pop_size+1)=pop_size+1;
            pop(2,pop_size+1)=1;
            pop(3,pop_size+1)=1;
            pop(4,pop_size+1)=0;
            pop(5,pop_size+1)=0;
            pop(6,pop_size+1)=1;
            pop(7,pop_size+1)=sc;
            pop(8,pop_size+1)=0;
        end
    end
end

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```

        pop(10,pop_size+1)=a;
        pop(9,d)=1;
        pop(10,d)=a;
        a=a+1;
    end
end
pop_size=size(pop,2);
d=d+1;
end

pop(1,1:pop_size)=1:1:pop_size;

pop(4,1:pop_size)=0;
pop(5,1:pop_size)=0;

pop(6,:)=pop(6,:)+1; % the individuals age and change their age class

for i=1:pop_size
    if (pop(9,i)~=0)&(pop(9,i)<4) %age the mum tracker and reset it if the calf is older than 4
        pop(9,i)=pop(9,i)+1;
    else
        if pop(9,i)==4
            pop(9,i)=0;
        end
    end
    if (pop(6,i)>age_maturity)&(pop(3,i)==1)
        pop(3,i)=2;
        pop(2,i)=1+unidrnd(2,1,1);%randomly assign the sex of maturing calves
        pop(7,i)=s1;
        pop(8,i)=r1;
    end
    if (pop(6,i)>age_threshold)&(pop(3,i)==2)
        pop(3,i)=3;
        pop(7,i)=s2;
        pop(8,i)=r2;
    end
end
c=sum((pop(2,:)==1)&(pop(3,:)==1));
am1=sum((pop(2,:)==2)&(pop(3,:)==2));
am2=sum((pop(2,:)==2)&(pop(3,:)==3));
af1=sum((pop(2,:)==3)&(pop(3,:)==2));
af2=sum((pop(2,:)==3)&(pop(3,:)==3));

end
%figure
%plot(1:Y,population(1:Y),1:Y,adultfemale(1:Y),1:Y,oldfemale(1:Y),1:Y,calf(1:Y))
%xlabel('Year')
%ylabel('population size')
%legend('Population size','adult female','old female','calves')
abundance(model,1:Y)=population(1:Y);

hold on;
plot(1:Y,population)
xlabel('Year')
ylabel('population size')
end

save(savefile, 'abundance');

```