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Review Article

# Life processes of Killer Whales: A Mathematical Approach

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- Movement modelling

**Abstract**

As an apex predator in many marine ecosystems, Killer whales (KWs) are an important candidate for population dynamics studies. Anthropogenic activities like discharge of toxic chemicals, mechanical disturbances created by ships, coastal urbanization etc. influence the health, behaviour and ecological dealings of these animal. This review paper attempts to analyse the mathematical models those capture interactions between KWs and various biotic plus abiotic factors. Population based Prey-predator models are the oldest tools used for evaluating the influence of KW predation on a single or multiple species of preys in a community. Often hydrophobic chemicals released in marine water are affecting KWs fatally hence a gamut of models has been proposed for estimating bioaccumulation of such chemicals. Similarly, whale watching is another detrimental activity that has been modelled by many research groups. However, due to their large size, multifaceted physiology, social behaviour, long span of life and wide migration field, each KW is quite distinct from the other. A straight forward model like average distribution coefficient of chemical species is often inadequate to predict levels of persistent chemicals in a population of KWs. Hence, agent based models are evolving on a continuous basis to study abiotic interactions like predicting changes in toxin levels temporally as well as spatially in the animals. Beside these mathematical models, some frameworks to study the movement of the animal have been represented in this paper. Technological advancement of telemetry and availability of sophisticated mathematical tools like Fractal analysis is expanding the scope of studying movement related aspects of the KWs.

## ABBREVIATIONS

KW: Killer Whale; GI: Growth Indies; AI: Abundance Indices; MI: Mortality Indices; FR: Functional Response; ODE: Ordinary Differential Equation; IBM: Individual Based Model; ALI: Aleutian Islands; EBS: The Eastern Bering Sea; POPs: Persistent Organic Pollutants; PCB: Polychlorinated Biphenyl; CRW: Correlated Random Walk; SSM: State-Space Model; CGE: Computable General Equilibrium; GEEM: General Equilibrium Ecosystem Model

## INTRODUCTION

Killer whale (*Orcinus orca*), the large marine mammals are unique in many ways; they are complex physiologically, exhibit sophisticated social interactions, lives in diverse marine habitat, and consumes a variety of preys starting from small fishes to large sea mammals [1-4]. KWshave attracted many scientific studies in the field of ecology because of their important and complex role in maintaining balance in an ecosystem [5,6]. Climate change [7], human activities like fishing [8], whale watching [9], influx of pollutants in sea water is affecting the behaviour, physiology and often survival of these large mammals [10]. Therefore, further intensification of studies on effect of these environmental factors on the animal has happened [11-16]. Because of large size (6- 10 tonnes), long life span (on an average male; 31 years and females; 46 years) complex physiology, extraordinary manoeuvring capability (speed above 56 km/h and can travel travels 100 kilometres in a day), and presence in extreme marine locations, KWs are difficult to study in native condition [3,17]. Capturing and de-capturing of these mammals is also problematic due to ethical and regulatory constraints [18]. General observations are killer whales die younger in captivity as compared to their native habitat [19]. Some of the member types like *resident* KWs of North Pacific sea are listed as endangered species [20]. Hence any experimental study need to be innocuous for the animals and requires regulatory clearance. Such restrictions in experimentally studying the animal have invoked effort in developing theoretical frameworks.

Mathematical models are useful tools for addressing various issues about a class of organism like their individual and social behaviour, interaction with other species in an ecosystem or impact assessment of environmental changes. From the ecological prospective prey-predator models are the most important one. Typically, various differential and difference equations are used for depicting population change of many species interlinked by direct consumption [21]. Individual based models emerged as the natural extension of these Lotka Volterra type models to include the mechanism based relation between animals especially for multiple species interactions [22]. Another important mathematical tool Markov's chain is a stochastic modelling system that is applicable for predicting a process based on current state of the process. This technique offers great opportunity to introspect movement of an organisms and related aspects like individual behaviour and interaction with other organisms or environment [23].

Prediction of fate of POPs in KWs exhibit multiple challenges. The chemicals enter directly via tissue absorption as well as indirectly through consumption of prey. That is why bio-concentration, bio-accumulation, and bio-magnification are always difficult to predict for a highest trophic level animal like KWs [24]. The difference of physiology with sex of the animal and distribution of hydrophobic chemicals in the body fat and tissues throughout the life span causes high degree of error in the estimation of average concentration in terms of per kg body weight (or lipid weight) [25].

This write up reviews the existing mathematical models with killer whales proposed by various research groups and present some models that can be further used in case of the species to elaborate many biological phenomena of broader interest.

## MODELS FOR DEPICTING BIOTIC INTERACTION

### One to one interaction between killer whale and single prey species

Marine mammals like KWs are at the top of four trophic level food chain. Hence it is important to study their interactions with individual prey species [26]. Simplest approach for such study is empirical models to connect the biological parameters of KWs with abundance indices of a particular prey over a period. Ford et al. [27], has found empirical models between the growth indices (GI) of KWs and abundance indices (AI) of a prey Chinook salmon (equation 1) and that between mortality indices (MI) of KWs and the same prey abundance index (equation 2) with considerable correlations. The GI and MI were defined as ratio of the number of observed births and deaths respectively to the numbers expected from a population model. AI was calculated as the ratio of the total population of the salmon in a year and the time averaged population of the salmon over the study period. To account for the effect of possible predation the AIs was calculated with a lag of one year than the time point of calculation of the MIs and GIs. This model suggests specialized foraging habit of the KWs.

$$GI = 0.3385AI + 0.6012r^2 = 0.227 \quad T_D\left(r\right) = k_2 r^{-\infty} \tag{1}$$

$$MI = -2.6054AI + 4.0066r^2 = 0.777 \tag{2}$$

Often killer whales are held responsible for abolishment of large marine mammals like harbour seals. In this context, [28] used an IBM model to portray effect of KWs on other marine mammals. The model added features like age structure, energetics, and societal connotations to Lotka-Volterra type model to assess true prey-predator interaction involving KWs.

Srinivasan et al. [29], proposed an IBM using tour boat data of seeing KWs and dusky dolphin. It simulated the movement of both the predator (KW) and prey (dusky dolphin) in a marked geography of 1648 $Km^2$ area over a 210 days' period with the help of appropriate programming tool. For making the holistic model data (appearance data for the KW and dusky dolphin, hunting speed, resting speed, feed time, flee, hide, stalk time) used from various sources, like tour boat data, previous literature, and logical estimates. The author claimed the model could visualize the changes in prey behaviour to avoid predation unlike a classical Lotka-Volterra type model. The modelling process is indeed a promising one but restricted by data gaps. However, with the advancement of telemetry technologies such model could yield valuable information regarding prey–predator interaction.

### Modelling role of KWs as an apex predator in a community

KWs as the apex predators in their concerned ecosystem control the population dynamics of the species existing down the food chain. Not just their numbers but change in foraging pattern of these animals can influence community composition [30]. There was interesting evidence that with even increased predation by KWs, the ecological status of an unconsumed prey population might thrive [31]. However, in case of KWs scanty mathematical modelling effort has been made for evaluating their roles in a community.

To explain shift of foraging preference of KW from large whales to sea lions and finally to sea otters, multi-prey functional response FR can be referred [6]. The model [6] states the relative number of consumption of two available preys ($C_1/C_2$) is product of relative number of attacks by the predators ($Z_1/ Z_2$) and that of initial population of the preys ($n_1/n_2$) or in other words $C_1/C_2=Z_1n_1/Z_2n_2$ [32]. Ecologically, when a predator switches from second to first species then the condition is $Z1/Z2 > n_1/n_2$. Switching is generally thought to be a mechanism to revive the depleting prey population so that both the preys can co-exist [33]. However, in case of extinction of pinniped in North Pacific switching of prey by KWs did not result ecosystem restoration. Van Baalen et al. [34], hypothesised a top-down model considering sub-regions in an ecosystem containing different preferred preys. Predator can follow either of the sub-regions randomly leading to system instability. Similar hypothesis is supported by Kimbrell and Holt [35,36], but with a IBM model approach.

In a marine community interaction between the apex predator and the subsequent next level consumer is an important ecological phenomenon to study. Addition of a meso-predator species in classical two species prey-predator model provides important information about KWs ecological prospective like restoration strategy for endangered KWs and effect of abundance or depletion of a competitive prey (meso-predators) [37]. The model is represented by a set of ODE (equations 3a-c) involving the population of Prey (P), Meso-predator (M), and an Apex predator (A). The main feature of the model is a preference factor (β) for the prey between the meso- and apex- predators. Where 0 and 1 value of β represents respectively complete exploitive competition and no competition at all between the predators.

$$\frac{dP}{dt} = P(r\left(1-\frac{P}{K}\right)) - \alpha M - \left(1-\beta\right)a \tag{3a}$$

$$\frac{dM}{dt} = M\left(b\alpha P - \beta a A - \gamma\right) \tag{3b}$$

$$\frac{dA}{dt} = A\left(b\beta aM + (1-\beta)aP - d\right) \tag{3c}$$

Often in an ecosystem more than one species of KWs may reside. Interplay of more than one categories of apex predator of the same species could influence the food web in a complex way. For example, transient and resident are two categories of KWs co-exist in the open sea around British Columbia, Alaska and Washington State. Their feed and reproduction patterns are quite different. To make the situation more complex the primary feed of transients i.e., pinnipeds (*N*) compete for the primary feed of residents i.e., salmon (Figure 1a). Following model (equations4a-c) is proposed by Baird et al. [38], to find out direct interaction between the two apex predators and the prey.

$$\frac{dR}{dt} = r_R R\left(K_R - R - \alpha P\right)K_R \quad \text{(resident whales)} \tag{4a}$$

$$\frac{dT}{dt} = T\left(BCP - D_T\right) \quad \text{(transient whales)} \tag{4b}$$

$$\frac{dN}{dt} = r_N N\left(K_N - N - \beta R\right)K_N - CNT \quad \text{(pinnipeds)} \tag{4c}$$

where $r_R$ and $K_R$ are the intrinsic rate of increase and carrying capacity, respectively, for resident whales; $r_N$ and $K_N$ are the equivalent values for pinnipeds; R and Tare competition coefficients between pinnipeds and resident whales, and vice versa; C is the number of pinnipeds captured per unit time per unit pinniped density by an average transient whale; B is the efficiency with which transient whales consume and assimilate pinnipeds; and $D_T$ is the density-independent death rate of transient whales. The analysis of the model revealed that equilibrium population of residents' upsurges with more abundance of transients whereas that of transients down surges with more abundance of transients. But this conclusion ignored the indirect interaction between the two types of KWs due to competition of between the meso-predator pinnipeds and salmons for smaller fishes (Figure 1b). Hence the authors Baird et al. [38], have modified the said model into a two prey and two predator version (equations 5a-d) by including population of the salmons. The modification further revealed an indirect mutualism between the two types of KWs i.e., increase in abundance of either of the two will affect abundance of the other positively. However, the mutualism could not be supported with actual observations but it laid down a background for studying/managing multiple types of KWs in a particular ecosystem.

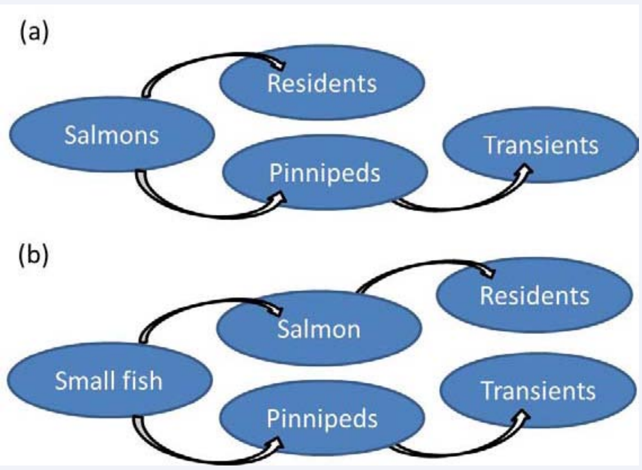


**Figure 1** Competing predators in a food web where (a) pinnipeds and residents killer whales compete for salmon and other fish and (b) pinnipeds compete with salmon for smaller fishes where transient killer whales remain as consumer of pinnipeds. (Adopted from Baird et al., (1992).

$$\frac{dR}{dt} = R\left(B_R C_R S - D_R\right) \quad \text{(resident whales)} \tag{5a}$$

$$\frac{dT}{dt} = T\left(B_T C_T N - D_T\right) \quad \text{(transient whales)} \tag{5b}$$

$$\frac{dN}{dt} = r_N N\left[1 - \left(\frac{N}{K_N}\right) - \left(\frac{\propto S}{K_N}\right)\right] C_N NT \quad \text{(pinnipeds)} \tag{5c}$$

$$\frac{dS}{dt} = r_S S\left[1 - \left(\frac{S}{K_S}\right) - \left(\frac{\beta N}{K_S}\right)\right] C_R SR \quad \text{(salmons)} \tag{5d}$$

Often KWs are perceived as threat to commercially important fish stocks and occasionally they have been captured or killed to prevent the fisheries [2,39,40]. Depredation by KWs in reserve waters (for other endangered species) or fisheries on some commercially important preys can be modelled as equations 6 a and b. Depredation data for five different prey fish by KWs was collected from 70 catching stations over a period of 13 years.

$$\log\frac{p_{ij}}{1-p_{ij}} = \beta_0 + t_i + S_j \tag{6a}$$

$$\log\frac{p_{ij}}{1-p_{ij}} = \beta_0 + S_j + \beta_1 t \tag{6b}$$

In the model, the $p_{ij}$ is the proportion of the depredate prey over time. A binomial response variable was considered which took 0 and 1 values when respectively no station was depredated and when at least one station was affected. The response variable was correlated linearly with the study year and station via a logit function {log[$p_{ij}$/(1 – $p_{ij}$)]}. The first equation (6a) relates the average of annual means of across all years ($t_i$) and station means across all stations ($S_j$), and the second equation relates station means and a simple linear trend ($\beta_1$ slope) in the proportion of depredated station over the time of study. The model gives a framework for finding influence of KWs in fisheries.

## Economy–ecology model

Currently detrimental impact of various anthropogenic activities on ecosystem is a matter of concern for the policymakers and one of the challenges faced by the governments is the economic aspect of it. A balance system supports economy of a region however the relation between the food web and economy is often difficult to describe. Alaskan economy is linked with Aleutian Islands (ALI) and the Eastern Bering Sea (EBS) ecosystem (Figure 2). A CGE/GEEM (computable general equilibrium, general equilibrium ecosystem model, respectively) [41], hybrid approach was adopted to represent such linkage.

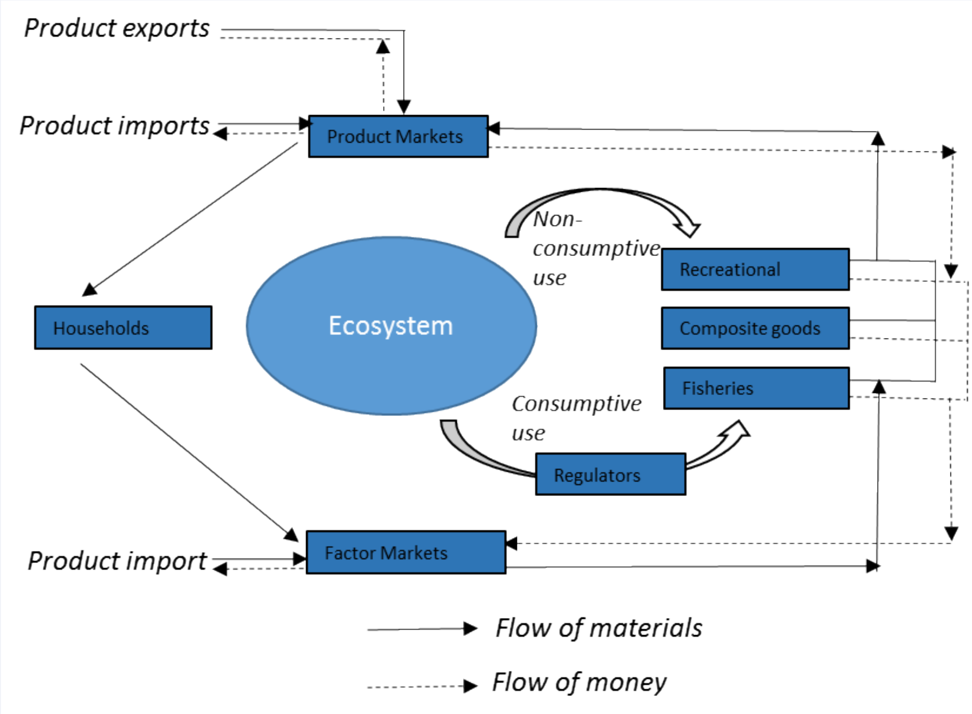


**Figure 2** Interlinked framework of economic-ecosystem consisting of flow of material (and services) plus money for the economy of Alaska and the marine ecosystem (essentially the animals) of Aleutian Islands and the Eastern Bering Sea. (Adopted from Finnoff and Tschirhart 2007).

Where each agent is linked with either of four types of processes; flow of money, flow of physical materials, consumptive or non-consumptive ecosystem flows. The ALI and EBS ecosystem has a four-trophic level food web where the KWs are sitting at the top. Adjacent trophic level members are related as prey-predators and follow energy dependent population dynamics. Population of KWs, Steller sea lion (prey for KWs), and sea otters (prey for KWs) are important for the tourism Industry in the region and therefore this non-consumptive flow of ecosystem is important economically. On the other hand, Pollock (consumed by Steller sea lion and sea otters) is harvested heavily for human consumption through fishery industry of the region. This consumptive flow of ecosystem also connects ecosystem to economics and usually regulated by governmental agency. So, CGE/GEEM hybrid system visualizes the impact on the economy of the region in case of any disruption of the links in the ecosystem. Empirical models were used to relate input factors of an industry to profit of each industry (fishery, recreational and composite goods) and for the ecological modelling mass balance followed by energy balance across the major species in the ecosystem were used.

## MODELS FOR STUDYING ABIOTIC INTERACTIONS

There is increasing number of factual evidences that the abiotic factors like pollutants, climatic shifts (global warming), fishing, whale watching (ship movement has detrimental effects on killer whales and other marine mammals. However, predicting effect of these abiotic factors on the species from laboratory scale studies is extremely difficult because of (i) compound effect of various chemicals (more than one type of contaminants) and physical (temperature) factors in their wild habitat (ii) long life span of these animals which makes long exposure time (iii) their existence in a heterogeneous habitat (iv) difficulty in observing physiological changes in their native condition and (v) regulatory barrier for some endangered species. Therefore, theoretical models are an effective tool to understand the effect of these abiotic factors on killer whales.

### Effect of contaminants on killer whales

A large array of organic compounds, heavy metals, persistent solids originating from industries, commercial farming, and domestic wastes are mixing in sea water systematically or accidentally. There are compelling evidences of direct or indirect effect of such contaminants on stimulus response system, reproduction and life span of killer whales [42].

Direct risk assessment of contaminants like persistent organic pollutants (POPs) in secondary predators like KW is very important. They are more susceptible to these compounds because of their slow growth rates and capability of storage of these hydrophobic compounds in their body lipid compared to the so called lean fishes. Further, complications arise due to bio amplification of such compounds in each trophic level [43].

POPs are lipophilic compounds so the simplest model for their estimation in KWs are based on distribution coefficient ($K_{o/w}$) of a target compound and ratio of the PCB concentrations in the KW and the environmental reference (RC; considered as concentration of the target compound in sediment or water column of a marine ecology). Empirical models like log (RC)=A log ($K_{o/w}$)+B has been put forward for modelling lipophilic toxicants in marine organisms where A and B are empirical parameters [44].

A simple individual based model has been devised to predict bioaccumulation of PCB in KWs by [45] (Figure 3). This model (equation 7) has been used for predicting PCB level in *resident* KWs of the North-eastern Pacific Ocean. Where $\alpha FC_f$ is the amount of PCB entering through the feed and $k_e C_w$ is the first order elimination rate of PCB via urination, excretion, plus metabolism in an individual KW over Δt time. $C_f$ and $C_w$ are the PCB concentrations respectively in the feed and in the KW. α is the assimilation fraction of the feed in the KW. $k_e$ is the specific rate of elimination. F is the feed rate of the KW which was calculated from power requirement of KW and the mean energy density of the feed. Required power can be again estimated from the empirical mass growth rate the organism. The model (equation 7) was adequate for males or non-reproductive females, but for productive females necessary amendments were done to include the additional feed intake due to gestation and lactation [45]. Though the bioaccumulation values predicted from the modified model was found to be on the higher side. However, it estimated the levels of PCB in KWs is much higher than the previous estimates therefore the present guidelines of PCB residues in sea water is inadequate and required to be revised for southern residents KWs.

$$C_{w,t} = C_{w,t-1} + (\alpha FC_f - k_e C_{w,t-1})\Delta t \tag{7}$$

Lachmuth et al. (2010), have proposed a more rigorous mechanistic model (equation 8) for closer prediction of the PCB bioaccumulation. The model accounted for the rate of PCB entering KW via aerial route ($k_a C_a$) and via variety of feeds ($k_d \sum(f_i C_{f,i}$ and the rate of PCB exiting the animal through various physiological processes (Figure 4). For calculation of the parameters secondary mass balance models were used. The concentration of PCB ($C_{w,l}$ was normalized for the lipid weight of the KW. The model was used for both finding out ecological risk index (ERI= $C_w/C_{crit}$ ) and Biota Sediment Accumulation Factors (BSAF = $C_w/C_s$ ) where $C_{crit}$ is the prescribed critical PCB concentration in KWs and $C_s$ is the PCB concentration in the sediment [46].

$$\frac{dc_{w,l}}{dt} = k_a C_a + k_d \sum(f_i C_{f,i}) - (k_0 + k_u + k_f + k_g + k_p + k_l + k_m)C_{w,l} \tag{8}$$

This model had provision of including differences in bioaccumulation of PCB due to age and gender in KW. However, the main two shortcomings of the model are steady state assumption and inadequate considerations of the dynamic role of sediment reserve of PCB.

The obvious next improvement in modelling of POPs in KWs should be a food web based model. Such models are required for more realistic assessment of POPs in KWs and include the indirect effect of these toxicants on the KWs. Apart from direct tissue toxicity of these contaminants, they cause behavioural changes,

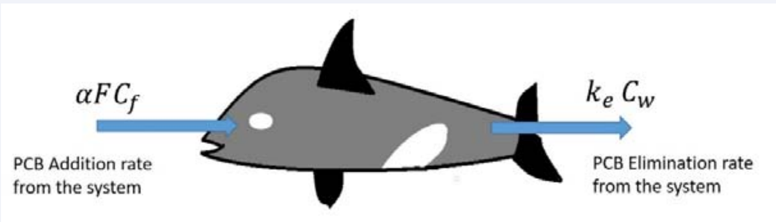


**Figure 3** Simplified depiction of bioaccumulation of hydrophobic compounds in killer whales. Where Cf and Cw are the PCB concentrations respectively in the feed and in the KW. α is the assimilation fraction of the feed in the KW. ke is the specific rate of elimination. F is the feed rate of the KW.

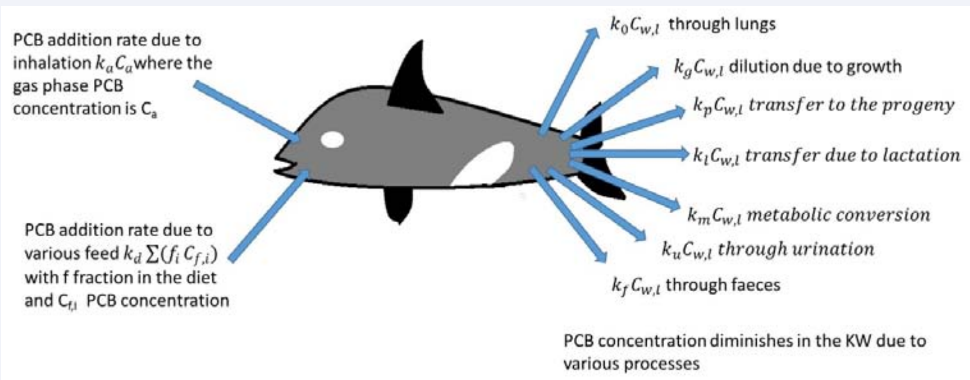


**Figure 4** Mechanistic representation of bioaccumulation of hydrophobic compounds in killer whales for prediction of the compounds.PCB enters in KW via aerial route ($k_a C_a$) and via variety of feeds $k_d \sum(f_i C_{f,i}$ and the rate of PCB exiting the animal through various physiological processes with specific rates $k_0$, $k_g$, $k_p$, $k_l$, $k_m$, $k_u$ and $k_f$.

alteration in competition and predation pattern which leads to drastic change in composition of the biota in an ecosystem [47]. A modelling process has been suggested in evaluating distribution of toxic molecules among all the organisms connected in a marine food web [48]. Of course, such models contain large number of parameters and their values are difficult to plug in.

In the context of modelling effect of lipophilic pollutants on KWs, particularly oil spills require special mention. Accidental blast/sinking of oil tankers, leakage from ships, and during wars have caused release of petroleum based hydrocarbons in many marine locations. Oil spills may induce fatal toxic effect in KWs [49] and moreover their effect on the higher trophic level organism is difficult to study because of multiple mass transfer processes and heterogeneous phase reactions involved in oil spills. Unified physical, chemical and biological processes determine fate of spilled oil in sea water. The oil phase can be distributed into vapour phase, into smaller droplets or emulsions, in solid phase as desorbed portion and eventually converts into smaller molecules chemically (like photo-oxidation) or biologically (by microorganisms, plants or animals) (Figure 5). It is estimated that within just 10 min after the contact, 1 ton of oil can form a 10mm layer over 7850 square meter of water surface. Most portion of the oil forms emulsion (~ 80 %) which can stay in the region intact even up to 100 days the remaining major fraction gets adsorbed in solid particulates [50]. Once the fraction of oils solubilizes they can enter directly or indirectly into the marine organisms including KWs. Therefore, essentially physical modelling of the fate of the oil phase after the oil spills is to be connected with the biological models to simulate the after math of oil spills on marine mammals. Two-dimensional or Three-dimensional hydrodynamic models were derived from Navier-Stokes equation with appropriate assumptions for describing the oil spill after math. Many authors have used efficient simulation techniques to solve these complex models [50].

### Modelling effect of physical activities

It is well known now that the mechanical disturbances, sound, and direct collisions due to marine vehicles are causing serious health and behavioural issues in KWs. In extreme case, these events lead to death of the animals.

A typical logistic equation has been used for finding effect of the physical disturbance on KWs population (equation 9)(51)

$$\frac{\Delta n}{\Delta t} = rn[1-\left(\frac{n}{K}\right)^{m}] \tag{9}$$

The statistical analysis suggested the presence of whale watching seriously affect carrying capacity (K) for a killer whale pod. Mechanistically, noise and disturbance produced from whale watching boats can modify KWs habitat in many ways like increasing energy requirement of the animal because of additional travel, reducing the prey search location due to noise, reducing the capability of combined foraging through echolocation etc. Potential Biological Removal= $F_r n_{\min}^{0.5} r_{\max}$ was recalculated and suggested to be lesser than then current default value. Result obtained by the authors [51], could provide guidelines like modification of fleet size, watching direction etc. for sustainable whale watching with respect to KWs.

## MODELS FOR TRACKING OF KILLER WHALES

Movement of animals is indeed a basic activity behind most of the essential needs of their life process like food, stress resolution, adaptation in a habitat, and reproduction. Importance of studying the movement of animals has been realized since the early days of biology however it is only in last fifty years advanced systems to study and interpret the intricate movement patterns of animals are available. The physical data acquisition related to movement of organisms in complex environment and sophisticated mathematical modelling techniques to interpret the data are required to qualitative as well as quantitative assessment of movement of large sea mammals like killer whales. Because they are not only distributed in a wider marine ecosystem but also does not require a finite interval for breeding in land like seals. The devices for tracking KW can be telemetry

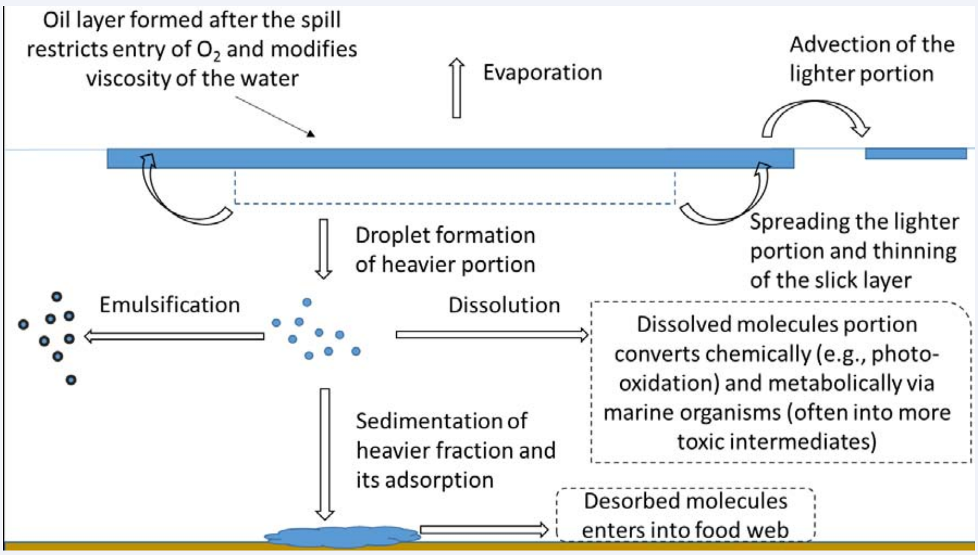


**Figure 5** Fate of hydrocarbon released in marine environment.

devices or tags, passive sonar arrays, active sonar systems, or their combination. Radio tags, ARGOS and GPS satellite tags have improved the accuracy of the spatial data and the resolution. Detail discussion about each of these technologies is out of scope. However, this remotely acquired data of animal movement is highly stochastic in nature and meaningless without proper modelling or statistical analysis.

A phenomological model is an obvious choice to analyse the movement data for generating meaningful conclusions but because of their complexity statistical models are more popular. Animal movement data is essentially locating an animal in two dimensional or three-dimensional space at different time intervals. The location data provides different estimates or movement matrices like velocity, step lengths, compass directions, turning angles etc. (Figure 6). Now any model explaining these data points consist of two aspects the mechanism for the movement process and a statistical framework to analyse the observation. In order to select appropriate model for a given study the characteristics of the data need to be known like the spacing of temporal data (regular or irregular) and level of error in detection of location.

For a regularly spaced location data discrete models (e.g., discrete time random walk model (CRW), state-space model (SSM)) are used whereas models like velocity based or diffusion-advection are suitable for irregularly spaced model.

Considering the unavoidable error associated with position estimation in existing telemetry methods of KWs state-space models are more dependable [52]. The general framework of such models [52] is given below;

$$X_t = g\left(X_t - 1, n_t\right) \tag{10a}$$

$$Y_t = h\left(X_t, \varepsilon_t\right) \tag{10b}$$

Where $X_t$= ($X_{longitude,t}$, t, $X_{latitude,\ t}$) describes the actual position of an animal at time $t$ and $Y_t$ describes the observed state of the animal. Equation 10a has an error term $n_t$ representing natural randomness in the movement of the animal whereas $\varepsilon_t$ is the error associated with the observation method (e.g., the specific telemetry method). However, this basic model is amenable for modification to deal with more complex kinematics.

For an irregularly taken location data for KWs correlated random walk model (CRW) are suitable [53]. Durban and Pitman [54], have suggested a CRW model where the velocity could be estimated by a random picking of step length and turning angles from an empirical distribution. Bayesian piecewise regression model was used to calculate average velocity of an animal from the velocity–time data. The conclusion from the model was trips to warmer water helps KWs in maintaining body heat with the less expense of metabolic energy.

Predation pattern or effect of prey response on movement of KWs has been studied using hi-tech observation studies [55,56], but its modelling is still a challenge. A hidden Markov model (HMM) can be adopted to describe diving behaviour of whales. In the model for each dive (time between successive breath), maximum depth, total vertical displacement number of tail flapping, mean vertical speed, dispersion of pitch, roll and heading were recorded. In addition to that acoustic data and visual vertical motion could identify four distinct types of dives in whales [57].

Scharf et al. [58], has proposed a Bayesian hierarchical model assuming social network based movements of KWs. The model predicts subsequent position of an animal at a time point based on previous position and social interactions like attraction between two animals plus alignment of the individual via a Gaussian random vector. The model was validated for explaining social behaviour of small population of KWs using telemetry data.

One of the latest mathematical techniques to model motion of animals is Fractal analysis. Fractals are shapes or processes without any characteristic length unlike Euclidean objects (e.g., sphere with diameter as characteristics length [59]. The typical random walk associated with movement of animals acquires two dimensions in Euclidian space therefore represents fractal dimension 2. This is even more promising for animal movements in 3D with tortuous path. One example of such model is equations

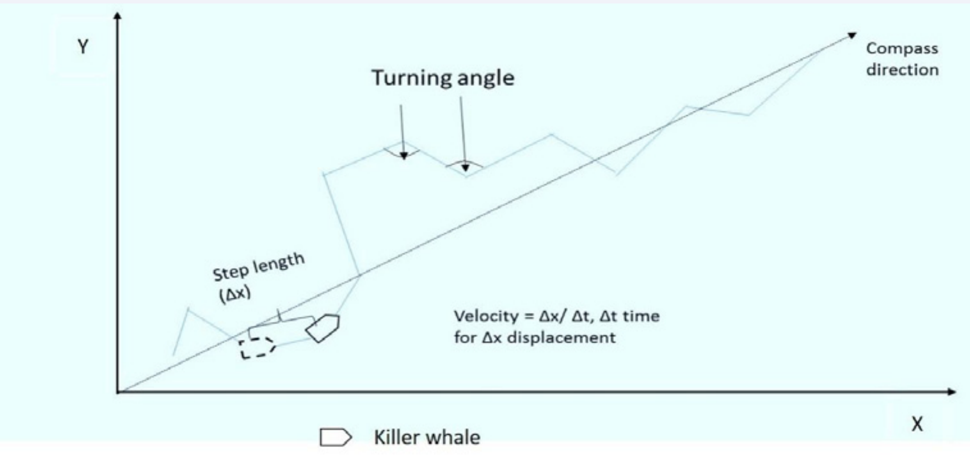


**Figure 6** Movement matrices of tracking motion of KWs or whales in a dummy plot (faded line is showing the path of KWs motion for which each node is the position of the animal at a particular time point).

11a-b [60].

$$P\left(t \le T_D\right) = k_1 t^{-\varnothing} \tag{11a}$$

$$T_D\left(r\right) = k_2 r^{-\propto} \tag{11b}$$

where $k_1$ and ϕ are characteristics constants can be estimated from the linearized (log-log) equation. Equation 11b can be derived from equation 11a, where $k_2$ and α are characteristics constants, $r$ is the rank of duration of a particular dive $T_D(r)$ in a series of dives in descending order. The model could explain influence of sea kayaks on the diving patterns of killer whales.

## CONCLUSION

Indeed mathematical models are excellent tools for testing of hypothesis related to various aspects of KWs starting from internal factors like behaviour, metabolism etc. to external factors like biotic and abiotic factors of the environment the animals. This paper has reviewed three significant categories of models and highlighted their importance as well as limitations. Unlike smaller animal species, KWs show considerable heterogeneity among themselves even in a single pod, variation in physiology throughout their life cycle, specialized response pattern, and environmental homogeneity due to large movement space. This complexity associated with the animal demands Individual Based Models for more realistic description of different phenomenon pertaining to them. Often cross modelling approach or combination of two different models is required to bring fidelity in model prediction. With the development of computational tools, for modelling of complex tracking of KWs sophisticated modelling techniques like Fractal Analysis would be popular.

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