Understanding the ecological effects of whale-watching on cetaceans

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Introduction

Whale-watching is a potentially sustainable use of cetaceans and an economically viable alternative to whaling and has become a major contributor to the tourism sector of many countries (Hoyt, 2001; O’Connor et al., 2009). Whale-watching also has the potential to improve people’s attitude toward the marine environment, and promote public awareness and support for the conservation issues that targeted species face (Duffus & Dearden, 1993). However, whale-watching can put cetaceans at risk of being harassed and injured by an unknown number of unpredictable impacts which can pose a risk to the viability of the targeted population, as well as the whale-watching industry itself.

Reported effects of human disturbance on cetaceans cover a range of taxa, including many odontocete species and several species of mysticetes (see Chapter 16). Even though many studies have shown that whale-watching can cause both short-term negative effects on cetaceans (Bejder et al., 2006; Fortuna, 2006; Lusseau et al., 2006b), few studies have focused on explaining the underlying cause, or ecological and evolutionary mechanisms for these effects (Prid & Dill, 2002). Understanding how human interactions affect wildlife is crucial for the sustainable management of any nature-based tourism activity. This chapter addresses the ecological foundations of whale-watching disturbance on cetaceans. It gives an overview of the documented impacts of whale-watching on cetaceans and compares this to observations of natural predation. It then tries to explain how whale-watching is perceived by the animals to understand the underlying ecological and evolutionary basis for these responses. It goes on to discuss different factors that are likely to influence the response of animals to whale-watching. We then discuss the long-term effects of whale-watching on cetaceans by following the mechanistic link between behavioural effects and vital rates within an energetic framework. Ecological and biological constraints to the ability of cetaceans to cope with disturbance are discussed as well as their implication for long-term vital rates.

The effects of human disturbance on cetaceans

Human disturbance is defined by Prid and Dill (2002) as a deviation in an animal’s behaviour from patterns occurring without human influences (see Blanc et al., 2006 for other definitions of disturbance). A large number of studies exist that show that cetaceans are disturbed by whale-watching, even though this is a non-consumptive activity.
(Tremblay, 2001). Frid and Dill (2002) explain this by arguing that animals perceive humans as predators and respond to human presence in the same way as in the presence of natural predators. Many cetacean populations do face predation risk from a variety of predators (Visser, 1999; Heithaus, 2001; Ford et al., 2005) and it has been proposed to be the basis for migratory behaviour in mysticetes (Corkeron & Connor, 1999). Therefore, cetaceans have evolved a variety of behavioural strategies to respond to perceived predation risk and it is within this context that they respond to the introduction of novel stimuli (i.e. whale-watching boats) that can be hazardous.

Short-term effects

Short-term behavioural responses towards whale-watching boats are often used to look at the effects of human disturbance on cetaceans, as they are often considered the most direct and hence sensitive measurement of the effects of human disturbance, as well as being relatively easy to measure in the field (Beale & Monaghan, 2004a). Cetaceans respond to whale-watching boats by altering their behaviour in a vertical or horizontal plane, or both. Vertical avoidance means that cetaceans spend less time at the surface, by increasing the depth and duration of dives (Nowacek et al., 2001; Lusseau, 2003b). Horizontal avoidance can be expressed by an increase in swimming speed and frequency of heading changes, to outrun or outmanoeuvre (confuse) the whale-watching boats (Williams et al., 2002b; Lundquist et al., 2012).

Because the vertical and horizontal movement of cetaceans is closely related to the activity they are engaged in (e.g. socializing animals spend more time close to the surface than when travelling), different activity states will differ in their susceptibility to whale-watching boats. Thus, whale-watching boats have been shown to affect the activity state of cetaceans (Lusseau, 2003a; Christiansen et al., 2010; Lundquist et al., 2012). Whale-watching also influences the trade-off processes between perceived predation risk and environmental and social factors, which affects distribution patterns (Allen & Read, 2000; Lusseau, 2005) and group dispersion (Bejder et al., 1999; Nowacek et al., 2001). Finally, both the presence and the noise level of whale-watching boats can affect the vocalization patterns of cetaceans (NRC, 2003; Jensen et al., 2009). Many of the behavioural responses mentioned above have also been observed between cetaceans and natural predators (Visser, 1999; Heithaus, 2001; Ford et al., 2005).

Long-term effects

Because cetaceans are long-lived and relatively hard to study, only three studies to date, all on odontocetes, have been able to show long-term effects of whale-watching on cetacean vital rates (Bejder et al., 2006; Fortuna, 2006; Lusseau et al., 2006b). Two of these identified a decrease in female reproductive success to be the causal factor behind the long-term effects, one resulting in a decrease in population size (Lusseau et al., 2006b) and the other in a shift in relative abundance between two areas (Bejder et al., 2006). For mysticetes, Weinrich and Corbelli (2009) found no long-term effects of whale-watching boats on humpback whales’ (Megaptera novaeangliae) calving rate or calf survival. However, this could be because of a lack of proper controls. Therefore, to date, the long-term effects of whale-watching on mysticetes are unknown.

Non-visible effects

Another important aspect of human disturbance on wildlife is that animals can be negatively affected by a disturbance without showing any visible changes in behaviour (Beale & Monaghan, 2004b). Studies of birds have shown that animals can still show physiological responses, stress, to human disturbance without showing behavioural responses (Fowler, 1999; Beale & Monaghan, 2004b) and such responses can reduce breeding success (Carney & Sydeman, 1999). Very little is known about how stress is expressed in cetaceans, and how it can be linked to short-term behavioural responses to
disturbance. Wild dolphins showed elevated concentrations of cortisol and aldosterone, two stress hormones, following the encirclement by capture nets (Aubin et al., 1996). While stress can be beneficial in some situations, severe, prolonged or cumulative stress can lead to disease and negative effects on survival and reproductive success (Fair & Becker, 2000). In captive bottlenose dolphins (Tursiops aduncus) stress resulting from social instability was shown to contribute to documented mortalities and illnesses (Waples & Gales, 2002).

Explaining the effects of human disturbance on cetaceans

Predation risk

Predation is an important factor shaping the lives of K-selected species (Heithaus et al., 2009). Apart from predators having direct consumptive effects on a population, predators can also have indirect non-consumptive effects in the form of predation risk (Figure 13.1). Because animals are unaware of actual predation risk, their behavioural decisions will be based on the perceived predation risk. The cost of predation risk can be seen as a trade-off between investments in anti-predator activities (e.g. avoidance, vigilance or group formation) and other fitness enhancing activities (e.g. foraging, mating, parental care), to reduce predation risk (Brown, 1999). As several factors influence perceived predation risk (Figure 13.1), there are also several strategies that animals can use to minimize it, which can vary between species and geographical areas. What all animals have in common, however, is that this trade-off can never be one-sided. If the trade-off is biased towards fitness-enhancing activities, and the investments in anti-predator activities is low, this will lead to an increase in predation rate for the animals which will have direct negative effects on population dynamics. On the other hand, if investment in anti-predator activities is too high, other fitness-enhancing activities will suffer which can lead to negative effects on animal survival and reproductive success (Creel et al., 2007), and indirect negative effects on population dynamics (Gill & Sutherland, 2000).

Alternatively, high investment in anti-predator activities can lead to a reduction in physiological state (body condition), which might also lead to an increase in predation rate (Sinclair & Arcese, 1995) and direct negative effect on population dynamics. Therefore, the indirect effects of predation, in the form of predation risk, might in fact be greater than the direct effects of predation through consumption (Preisser et al., 2005), especially in cases when the predator also preys on other species or are consuming a relatively small number of animals of the target population (Wirsing, 2007). In the Greater Yellowstone Ecosystem, USA, wolf (Canis lupus) presence led to a decline in the recruitment of elk (Cervus canadensis) calves in the area. The decline was shown not to be a direct effect of predation by the wolves, but an indirect effect of predation risk which caused a decline in progesterone levels of female elks when they engaged in anti-predator behaviours (Creel et al., 2007).

Predation risk in the absence of predation

Cetaceans often respond to human disturbance in the same way they respond to natural predators (see above). The non-consumptive effects can cause the targeted animals to divert time and energy away from other fitness enhancing activities, as human disturbance can from an evolutionary perspective be likened to predation risk (Frid & Dill, 2002). But how can whale-watching be perceived as predation risk by cetaceans, when it poses such a small risk of injury? Dolphins have been shown to be able to distinguish between different species of natural predators (Irvine et al., 1973), so it should be expected that cetaceans can differentiate between a natural predator and a whale-watching boat. Anti-predator responses are general towards certain stimulus (e.g. rapidly approaching objects) and not predator-specific (Frid & Dill, 2002). Therefore, rather than the object itself, the behaviour of the object is what triggers the anti-predator response.
and animals make no distinction whether the stimulus comes from a natural predator or a non-lethal whale-watching boat, even if the latter source is new to the evolutionary history of the animals, as long as the stimuli that elicit the response are similar (Prid & Dill, 2002). This also illustrates the fact that animals make their decisions based on the perceived predation risk and not the actual predation risk, as the latter cannot be known by the animals.

Further, it is not necessary that predation consumes a high number of prey or that capture attempts occur often (high predator attack probability) or have a high probability of success (low prey escape probability) for a predator to cause a strong response of the targeted animals in the form of predation risk (Preisser et al., 2005). Dolphins in Shark Bay, Australia, showed strong anti-predator behaviours during time periods when tiger sharks (Galeocerdo cuvier) were present in the area, despite dolphins only constituting a minor component of the sharks’ diet (Heithaus & Dill, 2002). Further, in cases where hunting by humans has represented a historical real threat to some species over evolutionary time (i.e. commercial whaling), disturbance stimuli and true predation stimuli might be indistinguishable from the perspective of the animals (Prid & Dill, 2002).

Cetaceans are K-selective species, and therefore their life history strategy aims to maximize fitness by increasing survival probability rather than fecundity (Stearns, 1992). To maximize survival, cetaceans have evolved to minimize predation risk at all costs. Therefore, to maximize fitness, cetaceans will...
over-estimate risks rather than under-estimating them, as the individual costs of anti-predator behaviours are much smaller than the potential cost of predation itself (death) (Bouskila & Blumstein, 1992). This means that whale-watching, even though it is non-consumptive and has the same potential to cause strong responses of the targeted animals as natural predation and that habituation to non-lethal disturbance in general is unlikely. Furthermore, cetaceans might actually respond to associates the distant sound of whale-watching boats with the fast unpredictable behaviour of closer boats, and repeated exposure to whale-watching boats might even lead to a decrease in the threshold level at which a response is triggered (Frid & Dill, 2002), following the concept of sensitization (Bejder et al., 2009).

That cetaceans over-estimate risks further means that the presence of a stimulus (i.e. the presence of whale-watching boats), rather than its intensity (i.e. number of boats), will be the main trigger of a response. This was shown for elk in the Greater Yellowstone Ecosystem, USA, which responded strongly to the mere presence of wolves in the area by altering their habitat use on a very short time scale (2 hours) and at a relatively large spatial scale (radius 3 km; Creel et al., 2005). Silent kayaks elicited similar responses as power vessels for killer whales (Orcinus Orca), showing that boat presence and behaviour rather than boat type was the main source of the disturbance (Williams et al., 2011). Finally, given the life history strategy of cetaceans, it can also be expected that potential long-term effects of whale-watching will be on female reproductive success rather than adult survival, which the few long-term studies on odontocetes confirm (Bejder et al., 2006; Lusseau et al., 2006b; see above).

**Factors influencing the effect of human disturbance on cetaceans**

The perceived predation risk, and hence the impact of human disturbance, of an animal is influenced by a number of factors (Figure 13.1), of which the relative importance varies between species, populations and geographical areas. Some of these factors relate to the predator (i.e. whale-watching boat), while others relate to the individual being targeted. Predation risk is further influenced by the social structure of the species and the environment in which the targeted animal lives. All these factors influence predation risk, and will hence affect the anti-predator response of an animal, rather than predation rate per se, and the same is therefore expected towards human disturbance (Frid & Dill, 2002).

**Predator-related factors**

The different components of predation risk are affected by different factors related to the predator, and hence whale-watching boats (Figure 13.1). The predator encounter probability is affected by the abundance and distribution of the predator and is generally proportional to the predator density in an area (Heithaus et al., 2009). Thus, the encounter probability, or exposure rate, of whale-watching boats will influence the perceived predation risk of cetaceans, which will be determined by the number of whale-watching boats in an area as well as the temporal and spatial overlap between whale-watching activities and the distribution of the targeted population. The predator attack probability, as well as the prey escape probability, is affected by predator type (e.g. stealth versus chase, diurnal versus nocturnal, etc.; Heithaus et al., 2009), distance and number (e.g. group size; Beale & Monaghan, 2004b), duration and behaviour (Frid & Dill, 2002). Similarly, the perceived predation risk of cetaceans towards whale-watching boats is influenced by a number of variables. The response is inversely correlated with the distance to the nearest boat (Nowacek et al., 2001; Stamation et al., 2010). The response of cetaceans has also been shown to be affected by the number of boats (Stensland & Berggren, 2007; Williams & Ashe, 2007).

Predation risk can then be understood as a function of the number of predators and the
distance to them. The two parameters are inversely correlated, meaning that several predators at a far distance might trigger a similar response as a single predator at a closer distance (Beale & Monaghan, 2004b). The response of an animal is not triggered by the distance to the predator per se, but is initiated when the rate of change of the perceived distance to an approaching object exceeds a certain threshold (Frid & Dill, 2002). The rate of change of the perceived distance will increase if the size of the stimuli is larger and the approach is faster and more direct (the predator becomes visible at a greater rate). Following this theory, both the size of the whale-watching boat, as well as its speed and behaviour are likely to influence the perceived predation risk of the targeted animals. Also the time that the stimulus remains at closer distance to an animal will influence the perceived predation risk (Frid & Dill, 2002). Support can be found in the scientific literature which shows that the response of cetaceans to whale-watching boats is influenced by vessel type and behaviour, the latter being further divided into angle of approach, speed, duration of interaction and movement predictability (consistency) (Bejder et al., 1999; Nowacek et al., 2001; Williams et al., 2002a).

Even though some scientists consider sound to be the primary reason for responses of cetaceans to whale-watching boats (NRC, 2005), other studies indicate that it is far less important and that many other factors are involved (Williams et al., 2011). In pinnipeds, the flushing distance (seals entering the water) of seals in the presence of boats at a haulout was shown to be higher for kayaks and canoes than motor boats (Henry & Hammill, 2001). Apart from being silent, kayaks and canoes generally moved slower, had a lower silhouette, and stayed for a longer time close to the haulout than the motor boats. Thus the behaviour of the kayaks and canoes resembled that of a stealthy predator, which might be the reason why they were perceived by the seals as a higher predation risk compared to the noisier, more easily detectable and therefore more predictable behaviour of motor boats. This suggests that the behaviour, or more precisely the predictability, of the boats is the key component for a successful encounter between cetaceans and whale-watching boats (Williams et al., 2011).

**Individual-related factors**

It is likely that individual animals differ in their sensitivity, and thus response, to human disturbance as they live different lives, have different personalities, play different roles in their populations and vary in their exposure rate to disturbances (Beale & Monaghan, 2004a; Blanc et al., 2006; Réale et al., 2010; Figure 13.1). The trade-off process between predation risk and other activities is likely to be strongly influenced by the animal’s reproductive value (the expected future fitness; Lima, 1998), which in turn is influenced by the age- (Constantine, 2001), sex- (Lusseau, 2003b) and reproductive class (Nowacek et al., 2001). The body condition, or physiological state, of an animal will also influence the response towards human disturbance (Beale & Monaghan, 2004a; Réale et al., 2007). Healthy animals or animals in high-quality (resource-rich) habitats are likely to have sufficient energy reserves or opportunities to acquire energy to afford the costs of avoiding a disturbance by changing their behaviour than animals in poorer conditions or habitats which are more constrained by current requirements and cannot afford to change their behaviour (e.g. stop feeding).

Thus, an animal that is seemingly unaffected by whale-watching boats might actually be in such a poor physiological state that ecological (nutritional) constraints prevent it from engaging in anti-predator behaviours (Beale & Monaghan, 2004a). Poor physiological state may be due to natural (e.g. seasonal/migrational) or anthropogenic factors (e.g. pollution, hunting, whale-watching disturbance), or a combination of both. Individuals within a population can also have different temperaments, which are consistent behavioural differences between individuals resulting from differences in reproductive value and not caused by age-, sex- or reproductive class or physiological condition (Réale et al., 2007, 2010).
Different temperaments have different intrinsic predation risks associated with them (Jones & Godin, 2010). For example, some individuals within a population might be bolder and devote more attention to foraging than anti-predator vigilance, while others are more cautious and devote more time to being vigilant. Bolder animals will have a higher foraging efficiency, but also a higher predation risk (Bell & Sih, 2007), while cautious animals will reduce the predation risk at the cost of lost foraging opportunities (Jones & Godin, 2010). While natural predation would favour cautious individuals (Bell & Sih, 2007; Réale et al., 2010), whale-watching will favour bold individuals, as the perceived predation risk does not involve an actual risk of predation (there is no benefit with being more vigilant in the absence of a predator). Whale-watching may therefore work as a selective force working in the opposite direction of natural predation. Thus the response of cetaceans towards whale-watching boats will vary between animals within a population and even for the same individual at different times because the ecological constraints that the animal is subjected to might vary temporarily (e.g. time periods with high prey availability versus low prey availability).

Social factors

The prey escape probability, and hence predation risk, is also influenced by the escape tactics of the targeted animals, which is strongly influenced by factors related to the species social structure (Frid & Dill, 2002; Figure 13.1). Cetaceans can form non-mutualistic groups, called aggregations or schools, which are formed because of non-social factors (e.g. high food availability) and provide no larger benefit to the members of the group. Alternatively, they can form mutualistic groups, called groups, which are based on social factors and which can provide benefits to the members and therefore last for months to decades (Connor & Norris, 1982). In cetaceans, animals from different species can also come together and form what is known as mixed-species groups (Stensland et al., 2003). In a predation context, schools can have the benefit of a dilution effect, which decreases an individual's chance of being captured by a predator, and therefore the risk of predation. Forming groups is a way for animals to reduce predation risk once a predator is present by collective vigilance, collective defence and dilution of risk (Stensland et al., 2003; Czecel & Winnie, 2005).

Predation risk is believed to be one of the main factors (together with food availability) for group formation in cetaceans (Norris & Dohl, 1980). Further, the group size of cetaceans is generally the result of a trade-off between predation risk and intraspecific competition for food (food availability) (Heithaus & Dill, 2002). Therefore, cetaceans living in fission–fusion societies (e.g. dolphins) adjust their group size depending on the predation risk and their current activity. For group-living cetaceans it is also likely that the tolerance level, and hence response, of an animal to human disturbance will be influenced by the tolerance level of the other individuals in the group (e.g. an animal with a very low tolerance level triggers an anti-predator response of the entire group at a very low predation risk). Therefore, group formation might reduce predation risk on an individual level, but it might increase energetic costs associated with avoidance tactics on a population level (Blanc et al., 2006).

Cetacean calves are physiologically limited in their ability to dive and swim fast (Mann & Smuts, 1998), which can make them more vulnerable to predators. Because a calf is very much dependent on its mother, these physiological limitations will also set limits to the mother's behaviour and also her associations with other conspecifics. These limitations will influence both the calf's and the mother's exposure and vulnerability to predators, and thus the perceived predation risk. In Moreton Bay, Australia, humpback dolphin (Sousa chinensis) groups containing pairs of females with calves whistled significantly more (to maintain close contact) than those without, following periods of high boat noise from transiting vessels, suggesting that the perceived predation risk caused by the vessel noise is higher for females with calves than other animals.
(Van Parijs & Cokeron, 2001). Because females with calves and groups containing females with calves are more sensitive to interactions with whale-watching boats (Stensland & Berggren, 2007; Stastinon et al., 2010), it is not hard to imagine that predation risk in turn can have negative effects on the relationship between mothers and offspring, and therefore the reproduction success of the population (Frid & Dill, 2002).

In the presence of a predator, a mother can either decide to stay with her offspring, which will increase its chances of survival (decrease predation risk) but might decrease the chances of survival of the mother (increase predation risk). Alternatively, the mother can decide to leave her offspring, which will increase the chances of survival of the mother (decrease predation risk) but decrease the chances of survival of the abandoned offspring (increase predation risk) (Edwards, 2002; Frid & Dill, 2002). This trade-off will be influenced by the reproductive value of the mother (Frid & Dill, 2002) and thus the life history of the species. Human disturbance on cetacean females with calves has been shown to trigger the same trade-off process. Chases by tuna purse-seiners in the Eastern Tropical Pacific Ocean frequently lead to the separation between spotted dolphin (Stenella attenuata) mothers and calves (Edwards, 2002). The mothers tried to remain with the adult group of dolphins, in order to increase their own survival probability, instead of remaining with their relatively slow-swimming calves, which would have increased the calves' survival probability. Above this, avoidance behaviours caused by whale-watching boats will increase the energetic expenditure for both the mother and the calf. If the energetic increase for the mother is sufficiently large, she might need to redistribute energy from lactation into maintaining her own homeostasis, leading to a decrease in energy acquisition for the calf.

Environmental factors

Resource availability has a strong influence on animal decision-making under predation risk. In general, animals try to match their distribution to that of their prey and avoid areas where predation risk is high (Lima & Dill, 1990). Habitat selection is thus based on a trade-off between predation risk and resource availability in a way that minimizes the ratio between mortality risk and energy intake. An animal is more likely to keep foraging in an area with high predation risk if the prey availability in the area is higher, and the rewards of continuing foraging is enough to meet the costs of the high predation risk, compared to an area with lower prey availability, where the benefits of continued foraging will be low in comparison to the risk of remaining there (Heithaus & Dill, 2006).

Animal escape tactics, influenced by the landscape features (e.g. depth, turbidity, bottom substrate, number of refuges/cover, etc.) can also have a strong influence on predation risk by affecting the prey escape probability (Heithaus et al., 2009). Habitat attributes that modify the probability that the animal will be captured and killed during an encounter with a predator are called the intrinsic habitat risk (Heithaus & Dill, 2006). Therefore, within a habitat, predation risk is influenced by both the probability of encountering a predator and the intrinsic habitat risk. The intrinsic habitat risk of a particular area might be so low (e.g. due to high escape probabilities) that even though the predator encounter probability is relatively high in that area compared to surrounding areas, the animals reduce their overall predation risk by residing there, which paradoxically results in animals selecting areas where the relative predator density is highest (Heithaus et al., 2009).

That predation risk influences habitat selection indicates that disturbance by whale-watching boats can lead to changes in cetacean habitat use, which in turn can lead to increased intraspecific competition or an increase in predation rate by natural predators, which could have negative effects on population dynamics (Gill & Sutherland, 2000). For example, whale-watching activities might cause cetaceans to spend more time in low-quality habitats, resulting in increased intraspecific competition for food, as observed against
natural predators (Wirsing et al., 2007). As cetaceans cannot distinguish between perceived predation risk coming from a non-lethal whale-watching boat and that resulting from actual predation (Prid & Dill, 2002), whale-watching activities could also displace animals from relatively safer habitats to areas with higher rates of natural predation, without the animal necessarily becoming aware of the difference.

**Estimating the costs of human disturbance on cetaceans**

**Linking behavioural effects to vital rates**

The behavioural response of cetaceans towards whale-watching boats is the result of a trade-off process between the costs of the perceived predation risk (the avoidance behaviour) and the benefits from remaining engaged in a particular activity or occupying a certain area. The trade-off process is greatly influenced by the ecological conditions of the area occupied, which is likely to vary both spatially and temporally, leading to a complex response of the threshold level at which a behavioural response is triggered. While we have discussed the link between predation risk and behavioural effects, for management it is important to understand how short-term behavioural effects translate into long-term biologically significant effects on individual vital rates (survival and reproductive success), and ultimately population dynamics (NRC, 2005; Réale et al., 2007; Figure 13.2).

**Energetic effects**

Anti-predator activities all have energetic costs associated with them, either in themselves (e.g. increasing metabolic rate) or by taking time away from other energy-enhancing activities (e.g. foraging), or both (Williams et al., 2006). Predation risk can thus be seen as a trade-off between energy-consuming activities and energy-acquiring activities. Time allocation patterns (activity budgets) can be used to access the energetic costs of predation risk, and thus human disturbance, on cetaceans by comparing the time an animal allocates to different energy-relevant activities, such as energy acquisition (e.g. foraging), energy consumption (e.g. travelling) and energy conservation (e.g. resting) in the presence and absence of whale-watching.
boats (Williams et al., 2006; Wirsing et al., 2007). Energetic expenditure can increase if animals increase the swimming speed (Williams & Noren, 2009) and/or the frequency of evasive behaviours in the presence of whale-watching boats, while energy acquisition can decrease if foraging behaviour is reduced or halted (Williams et al., 2006). Some studies show that this latter effect is probably more likely to lead to long-term consequences than the former (Williams et al., 2006).

**Cumulative effects**

So far we have most particularly discussed the effect of individual interactions between whale-watching boats and cetaceans. Such short-term effects alone are unlikely to lead to long-term energetic effects for animals (Figure 13.2). For example, an animal might be able to compensate for an increase in energetic demands, or a decrease in energy acquisition, by increasing feeding and/or resting time when the disturbance is absent (Blanc et al., 2006). A migrating baleen whale targeted by whale-watching boats for a few hours while on its migratory route is therefore unlikely to be significantly affected by the interaction. However, if a disturbance becomes more frequent, the animal might no longer be able to compensate for the energetic costs, suggesting that the effects of whale-watching are cumulative rather than catastrophic. A resident population of dolphins targeted by whale-watching boats several hours per day throughout the year is therefore more likely to suffer biologically significant effects from the interactions (Lusseau et al., 2006b).

Whale-watching activities can also target individuals within a population disproportionately, with a preference for certain areas, behaviours and/or age-classes. Therefore, the overall exposure rate of an animal to whale-watching activities needs to be estimated in order to assess the long-term effects on bioenergetics and consequently vital rates (Constantine, 2001; Lusseau, 2003a). If whale-watching causes a long-term decline in population size the cumulative exposure rate for the remaining animals will increase, which in turn will lead to a vicious cycle that can lead to either extinction (Lusseau et al., 2006a) or desertion of the area.

**Area avoidance**

If the perceived predation risk caused by whale-watching activities is high, the only way for cetaceans to deal with the increased energetic costs of anti-predator activities might be to switch from short-term behavioural avoidance strategies to a long-term area avoidance strategy (Lusseau, 2005; Figure 13.2). Area avoidance means that the animals either temporarily move away from an area during periods when tourism intensity is high, or leave an area entirely to move to another area where they may remain (Bejder et al., 2006). Area avoidance differs from changes in habitat use because the former removes animals from the local breeding population through emigration, whereas the latter results in changes in the population distribution, but the local breeding population remains the same (however, maybe not the effective population size).

As for habitat selection under predation risk, there is a likely cost–benefit consideration behind an area avoidance decision. An area avoidance tactic will be triggered when the costs of remaining in a disturbed area exceed the benefits of staying there. The factors that determine the outcome of such a trade-off include the quality (resource availability, etc.) of the area that is currently being occupied, the quality and distance to other suitable areas, the relative predation risk between the two areas, the relative intraspecific competition between the two areas as well as the investment already made in the current area (Gill et al., 2001). The perceptual range of the species, which is the distance from which an individual can perceive these factors, will set the limits to these decisions (Zollner & Lima, 1997). An animal might also remain in a disturbed area simply because no alternative habitats are available. This might result in negative effects on individual vital rates and even population size, because the high level of predation risk effectively decreases the perceived quality of the habitat (even though
the actual quality of the habitat remains the same; Prid & Dill, 2002). Therefore, even if animals remain in an area where whale-watching is taking place, it may be that animals are affected by whale-watching activities (Christiansen et al., 2010) but that ecological constraints prevent them from leaving the area.

**Ecological and biological constraints to compensation**

Environmental variability will set constraints to the ability of animals to compensate for the energetic costs of human disturbance (Figure 13.2), by constraining their time activity budget (see Chapter 17). For example, if prey is distributed heterogeneously in an area and whale-watching interactions occur in a spot (or during a time period) where prey availability is high, an avoidance response (e.g. change in activity or habitat use) caused by whale-watching will carry a much higher cost than in areas (or during time periods) where prey availability is low. Animals living in areas where prey, or any other vital resource, is distributed heterogeneously will therefore be more constrained in their ability to compensate for whale-watching interactions than animals in areas where prey is distributed homogeneously and where they have more opportunities to compensate for a loss in energy caused by whale-watching.

Apart from the environmental variability setting ecological constraint on the ability of animals to compensate for whale-watching interactions, the life history of a species further sets biological constraints to compensation (Figure 13.2). Life history describes how an animal allocates resources to reproduction throughout its lifetime to maximize lifetime reproductive output given its survival probability (Sterns, 1992). A distinction is made between income breeders, which use current energetic income to finance reproduction, and capital breeders, which use previously stored energy to finance reproduction (Stephens et al., 2009). The two reproductive strategies have different energetic costs associated with them. For example, the amount of energy that income breeder females can invest in their offspring is directly related to how much prey they can consume during the lactation period and therefore they try to maximize the rate of energetic intake during the lactation period (Costa, 1993). However, an increase in the rate of energy intake also leads to an increase in foraging (and metabolic) effort. An income breeder strategy is therefore energetically relatively costly and consequently only exists in areas that are highly productive where prey is concentrated and predictable (Costa, 1993).

Capital breeders can separate lactation from foraging so females are able to accumulate the energy needed for lactation over a longer time period. This results in a lower daily energy requirement to finance reproduction. This strategy provides more flexibility to acquire energy and to invest energy in reproduction, which enables capital breeders to utilize highly dispersed, patchy and unpredictable prey resources (Costa, 1993). The capital breeding strategy is thus more economical. However, as body reserves are limited, this also limits the total amount of energy that the mother can invest in her offspring. In contrast, income breeders have a less energy-efficient reproductive strategy, but have no limit to the amount of energy they can invest in their offspring, as they can increase their net energy intake by increasing their foraging effort (Costa, 1993).

Most mysticete species undertake long-distance seasonal migrations between high-latitude feeding grounds and low-latitude breeding grounds and thus lactation is separated from foraging both spatially and temporally, meaning that they need to rely on body reserves to nurse their calves in the low productive breeding grounds (Kasuya, 1995). Odontocetes, on the other hand, generally have a relatively restricted habitat and are resident in the sense that they both feed and breed within the same area. The flexibility of capital breeding in acquiring energy and investing it in reproduction enables mysticetes to utilize crustaceans and schooling fish which are abundant seasonally far away from the breeding grounds, while
income breeding odontocetes need to rely on locally abundant and predictable resources of marine mammals or fish (Kasuya, 1995).

Mysticetes that have a capital breeding strategy are more likely to be severely affected by whale-watching boats disrupting their energy acquisition in their feeding areas (Stephens et al., 2009), because the foraging success in feeding grounds will set the limits to the amount of energy that can be transferred to their offspring in the breeding grounds, and thus the reproductive success. Conversely, because cetaceans are K-selective species, added energetic expenditures on the breeding grounds will also lead to re-routing of energy from lactation to homeostasis (to increase female survival probability), which will ultimately also lead to a decrease in calving success, and reproductive success. Odontocete income breeders, on the other hand, are likely to be more vulnerable to whale-watching boats while breeding (Stephens et al., 2009) as their foraging success at that time is directly linked to their reproductive success. Again, female odontocetes will sacrifice fecundity for survival, by allocating more energy to maintaining their own homeostasis, and thus survival probability, instead of investing it in lactation (reproduction) during interactions with whale-watching boats. Further, capital breeders are more likely to be able to cope with an unpredictable environment shaped by whale-watching boats than income breeders which are not as flexible in respect to energy acquisition and investment in offspring (Stephens et al., 2009).

Management implications

The effect of whale-watching activities on cetaceans can be minimized if the different factors that influence predation risk (Figure 13.1) are taken into consideration when creating guidelines or regulations for whale-watching. Apart from regulating the behaviour of the whale-watching boat itself (e.g. distance and speed), interactions with particular age-, sex- and reproductive classes or group compositions of cetaceans can be avoided (e.g. mother and calves), as well as interactions in areas where animals are likely to be more sensitive to disturbances (e.g. shallow areas or foraging habitats). Knowledge about the ecological and biological constraints to a population should be used to regulate not only the overall exposure rate (daily interaction time), but also where and when interactions should take place, so that the overall time that whale-watching boats can interact with cetaceans (and consequently the economic profit) can be maximized without causing long-term negative effects on cetacean vital rates.

Many of these aims can be achieved by the designation of marine protected areas (Hoyt, 2005; also see Chapter 19). Marine protected areas (MPAs) have been shown to be effective in protecting cetaceans from direct mortalities, such as fisheries by-catch (Gormley et al., 2012); however, with regard to non-lethal effects their design is often inadequate (Williams et al., 2009; Ashe et al., 2010). This chapter highlights many of the factors that need to be taken into account when designing MPAs for cetaceans to minimize the effect of non-consumptive activities. Some studies have already demonstrated that this can be done successfully. Ashe et al. (2010) used behavioural data of killer whales to identify which activities were most sensitive to human disturbance, and then evaluated how different habitats were used for these activities, to propose priority habitats to be protected. In a similar way, Williams et al. (2009) used behavioural information to evaluate the effectiveness of a voluntary no-entry reserve for killer whales by assessing habitat preference in a behavioural context and the population-level implications of that preference given threats from human activities. Thus, incorporating behavioural data into the selection of MPAs, as well as wildlife management in general, is crucial to minimize the non-lethal effects of whale-watching on cetaceans.

Conclusions

Fundamental to understanding the effect of whale-watching on cetaceans is understanding
that animals have evolved anti-predator responses that are general, and therefore make no distinction whether the stimulus that triggers a behavioural response comes from a natural predator or a non-lethal whale-watching boat. Cetaceans will therefore over-estimate risks, making habituation very unlikely to develop. Further, because animals make their behavioural decisions based on the perceived predation risk and not the actual predation risk, the perceived predation risk can often be high in situations where the actual predation risk is low or non-existent. The fact that the indirect effects of predation, in the form of predation risk, can exceed the direct effects emphasizes the need for wildlife managers to take non-lethal effects of human disturbance seriously. Documented long-term negative effects of whale-watching activities on cetacean vital rates further support this statement.

This chapter shows that the perceived predation risk, and thus avoidance responses, are influenced by a number of factors related to the disturbance stimuli, the targeted individual, the social context the animal lives in and the environment, and that these factors coexist in complex interactions with each other. Understanding how short-term behavioural effects of whale-watching activities translate into long-term biologically significant effects on individual vital rates, and ultimately population dynamics, is of central importance for managers. Time allocation patterns (activity budgets) relating to different energy-relevant activities can be used to link behavioural changes to bioenergetics. Knowledge of the overall exposure rates of individual whales to whale-watching activities can then be used to assess long-term effects on bioenergetics and consequently individual vital rates. Knowledge of the species’ life history and the environment in which it lives is necessary to evaluate biological and ecological constraints on compensation, and thus vulnerability.

This information is critical to the effectiveness of operator guidelines and the designation of MPAs. Furthermore, wildlife managers must understand, for example, that in mysticete species long-term effects are not readily detectable, but could affect reproductive success months in the future, at locations thousands of kilometres away. Knowledge of the mechanistic link between behavioural effects of whale-watching and vital rates is fundamental to this understanding, and more research should be directed towards these critical links.

REFERENCES


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