論 文 の 内 容 の 要 旨

論文題目　**Time budget and activity pattern of humpback whales, *Megaptera novaeangliae*, in the Northern foraging grounds**
（北方採餌海域におけるザトウクジラの行動時間配分と活動様式）

氏　　名　秋山　優

Chapter 1: General Introduction

Population size of humpback whale were greatly reduced due to massive overexploitation in the past. Currently, among the 14 distinct population, four are still protected as endangered and one is listed as threatened. Thus, better understanding is needed for conservation and management.

Humpback whales are large baleen whales which undergo annual migration between the foraging grounds at high latitude and breeding grounds at low latitude. When they are away from the foraging grounds, they generally cease feeding, therefore; the success of their survival and reproduction depend largely on energy store during the foraging period. Because resources and time are limited, there will always be a trade-off between various activities.

The two most important behaviors for the survival of animals are foraging and resting. This study, investigated these two most important behaviors, foraging and resting in addition to time budget of humpback whales in foraging grounds of Iceland, Norway and Canada, by attaching animal-borne accelerometers and video loggers directly on whales. Lastly, to further understand the depth selection of wild humpback whales, experimental study was conducted to investigate the effect of wave drag on cetaceans using a trained bottlenose dolphin.

Chapter 2: Adaptive foraging strategies of the Icelandic population

Humpback whales forage on densely aggregated prey using a distinctive feeding strategy known as lunge feeding. During lunge feeding, humpback whales accelerate towards a patch of prey and engulfs large amount of prey with water. This foraging style may induce drastic change in prey density in a single feeding event, therefore; the decision whether to leave or stay after each feeding in a single dive in response to this drastic change should have a significant effect on prey exploitation efficiency. However, whether humpback whales show adaptive behavior in response to the diminishing prey density in a single dive has been technically difficult to test. Here, the foraging behavior of humpback whales in response to change in prey density in a single dive was investigated and the efficiency of each foraging dive was calculated using a model based on optimal foraging theory approach which predicts the optimal patch residence time of predators in response

to patch quality. Using animal-borne accelerometers and video loggers attached to whales, foraging behavior and change in relative prey density in front of the whales were successfully quantified. Results showed a diminishing rate of energy intake in consecutive feeding events, and humpback whales efficiently fed by bringing the rate of energy intake close to maximum in a single dive cycle. Moreover, this video-based method also enabled to detect the presence of other animals around the tagged whale, showing an interesting trend of shortened patch resident time when other humpback whales were feeding in the same patch.

Chapter 3: Resting characteristics and strategy

Resting is an essential part of all life and lack of rest can be fatal. However, in the study of wild cetaceans, resting tend to receive less attention in comparison with foraging behavior and little is known. Therefore, resting characteristics of wild humpback whales were investigated. Resting was defined as immobile state, where swim speed is 0 ms^{-1} and no stroking for more than 1 minute. Resting was extracted from 10 out of 48 whales and showed that humpback whales rest horizontally at sea surface or underwater. The underwater resting is an interesting phenomenon as it seems more reasonable for them to rest at surface where they can continuously breath. So, the question is how and why they rest underwater. Body density of humpback whales are known to be denser than sea water, therefore; they are negatively buoyant. This indicates that humpback whales are controlling the air volume in their lungs to maintain neutral buoyancy while resting underwater. In order to investigate why they rested underwater, relationship between resting depth and wind speed were studied. The result showed an increase in resting depth with increase in wind speed. This suggested that when wind speed was low and sea surface was calm, humpback whales rested at surface, so they could constantly breath but when wind speed was high, and sea surface was rough, they rested underwater to avoid the unstable condition at the sea surface. However, the maximum resting depth was 28 m, so they never dove too deep because 28 m dive is enough to avoid the unstable condition at surface and there will be a cost of transportation to dive deep.

Chapter 4: Difference in time allocation of activities among populations

Humpback whales in foraging ground have strictly high demand for feeding because time for foraging is limited during the foraging period. Investigating how they allocate time between foraging and resting under this demand to optimize their fitness is an interesting topic. Previous studies indicated that activity patters and time budget is strongly correlated with environmental conditions and can show great variation within the same species among population. Thus, time budget and the daily activity pattern of humpback whales during the foraging period was compared among three populations. Behavior were separated in bouts of three categories, foraging bouts, resting bouts and the remaining as moving bouts. There was variation in time budget among three populations which may be due to difference in foraging seasons. Data of Iceland and Canada was taken during the early foraging season (June and July) therefore, the most common activity was foraging, and very little time was spent for resting. Data of Norway was taken during the late foraging season (January) and showed less foraging, and a highest ratio of resting behavior among the three populations. This study suggests that during the early foraging season, humpback whales rest less to

meet the energy requirement by spending longer time for foraging. Although when they have stored enough energy (late season), they decrease the foraging duration and rest longer.

Moving bout was the most common activity in Norway. However, the function of this phase is unclear. It may consist activities of various purposes, such as transit dives between the prey patch to some resting spots, searching for prey patch, or they may be executing Uni-hemispheric slow wave swim sleep. Although, further investigation and development might be needed to identify the activities included in moving bouts. Regardless, adaptive strategy was also seen in moving bouts. Humpback whales frequently used depth around 10 - 20 m during dives of moving bouts. The same question from chapter 2 arises again as to why humpback whales frequently use depth around 10 to 20 meters while they can continuously breath if they swim along the surface. The best guess is the effect of wave drag, a largest drag component acting on swimming animal at surface. In order to investigation the effect of wave drag on cetacean an experiment was conducted using a captive dolphin.

Chapter 5: Evaluation of wave drag on a swimming bottlenose dolphin

When animals move across the water surface, they push out surrounding water, creating waves. This work of wave formation is considered the largest drag component at the water surface and is known as wave drag. Cetaceans that need to return to the surface to breathe cannot avoid the effect of wave drag. Although, the effect of wave drag is estimated to be 5 times greater at surface but becomes insignificant at depth below 3 times the body diameter of an animal. Thus, by constantly repeating shallow dives at few meters below the surface when swimming, cetacean may avoid the effect of wave drag. The shallow dives of humpback whales observed around 10 to 20 meters in depth during the moving bout may be a way for them to avoid wave drag near the surface. However, no direct study has been reported on wave drag with animals swimming by its own effort. Therefore, by attaching animal-borne accelerometers to a dolphin trained to swim horizontally at water surface and at predefined depths, the effect of wave drag was estimated from the dolphin's stroking effort. The experiment indicated that body amplitude was significantly larger at the surface than at a depth of 3 m within a given speed range. This suggests that dolphins can swim with less effort at 3 m in depth than at surface because the effect of wave drag is insignificant at 3 m. In the case of wild humpback whales, the body diameter of humpback whale is reported to be 3.21 meters. Three times this body diameter will be around 10 meters. This completely matched with the depth which wild humpback whales were frequently using. Hence, it is very likely that during dives of moving bouts, humpback whales are frequently using the depth around 10 to 20 meters where the effect of wave drag is estimated to be insignificant.

Chapter 6: General Discussion

Present study is significant in various ways. First of all, this study specifically focused on activity patterns and time budget of humpback whales in the northern foraging grounds, in which two of the population (Iceland and Norway) are categorized as endangered species. No management or conservation act can be introduced without sufficient knowledge of the animal. Secondly, this study estimated the change in prey density in front of a humpback whale in time and place where feeding occurred and explored the foraging efficiency of

humpback whales in response to the changing prey density in a single dive. Without the biggest attempt to estimate the prey density using a video-logger attached directly to a humpback whale, none of this could have been accomplished. Moreover, the video-based method shed a light to explore not only the predator–prey interaction but one step further to predator–prey–competitor interaction which stimulats future research, reemphasizing the significance of monitoring and incorporating all possible information regarding the surrounding environment; as animals respond sensitively to the changes in surrounding situation over time. Thirdly, this study is perhaps the first to show quantitative evidence of humpback whales resting underwater. In all activities, there was an adaptive strategy to optimize their behavior. All of these are valuable information of humpback whales itself but also, as a major consumer of worldwide oceanic productivity, humpback whales will be a powerful tool for monitoring the marine ecosystem through changes in their behavior for the future.