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Cetacean movements in relation to the dynamics of the sound-scattering layer in the Azores

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Abstract

Patchiness is a key feature of pelagic ecosystems. Interactions between physical and biological processes result in variability in biological production and biomass over a range of scales in space and time. To survive in a spatially and temporally heterogeneous environment, predators must successfully locate and exploit dense concentrations of prey. Biophysical coupling at seamounts may lead to the formation of pelagic foraging hotspots, which can attract predators like cetaceans. However, the mechanisms linking physical processes, prey dynamics and cetacean foraging are complex and scale-dependent. The main goal of this dissertation was therefore to understand the dynamics of prey aggregations at seamounts and to determine if and how cetaceans exploit these foraging opportunities.

Active acoustic surveys were used to investigate the spatio-temporal dynamics of micronekton organisms (small epi- and mesopelagic fishes, cephalopods and crustaceans) on two seamounts (Condor and Gigante) in the Azores and in surrounding open-waters. At the same time, two hydrophones were deployed at these seamounts to obtain information on cetacean presence.

Our results demonstrated that Condor and Gigante seamounts significantly affect the distribution and dynamics of the micronekton. Strong aggregations of micronekton were a permanent feature above the summits of both seamounts, regardless of the season and diel period. This contrasted with reduced micronekton concentrations in the water column above the seamount flanks, which were lower than those measured in open waters just a few kilometres away. Over the summits, the micronekton community was vertically structured into a single, diffusely distributed layer, whereas above the slopes and in the open ocean, it formed two distinct layers: a shallow-scattering layer (SSL), distributed from the surface to approximately 150 m depth, and a deep-scattering layer (DSL), from ~ 350-650 m depth. The distribution and behaviour of the two layers varied with time of day but in opposite ways. The relative density of the SSL increased by ~5 times at night and organisms were more densely aggregated into a well-defined layer. As for the DSL, the daytime density was nearly the double of the nighttime density, with micronekton forming thicker and slightly denser patches than at night. These findings suggest that diel changes in the two layers most likely result from the nocturnal vertical migration of part of the DSL that merges with the SSL in the upper water

column. Micronekton present in surface waters would then be attracted or passively advected onto the seamount summits that would retain part of this community during the day. Therefore, seamounts may provide enhanced foraging opportunities for cetaceans through a combination of vertical migrations and local retention of prey.

The results of passive acoustic monitoring showed that dolphins were acoustically detected in Condor and Gigante almost every day, remaining 4 hours on average in the vicinity of the seamounts. The most frequently detected dolphin vocalizations were echolocation sounds, known to be associated with foraging behaviour. However, we found a clear diel pattern in dolphin acoustic activity, with higher vocalization occurrences at night. Taken together these results demonstrate that small dolphins consistently use Condor and Gigante seamounts to forage but they do so predominantly at night.

Further examination of micronekton and dolphin distribution patterns suggest that at night dolphins are exploring the highest prey aggregations found close to the summit seafloor and/or exploring the high micronekton concentrations available in surface layers above seamount slopes, consequence of the upward migration of organisms from the DSL to the SSL. These results suggest that foraging on higher concentrations of more aggregated prey close to the summit bottom during the day may not be energetically efficient.

This study contributes to a better understanding of the role of seamounts in shaping micronekton communities in oceanic environments and how this in turn affects the foraging ecology of dolphins.

Resumo

A existência de agregações é uma característica fundamental dos ecossistemas pelágicos. A interacção entre processos físicos e biológicos produz variabilidade na produção biológica a diferentes escalas espaciais e temporais. Para sobreviver num ambiente espacial e temporalmente heterogéneo, os predadores têm de localizar e explorar densas concentrações de presas. Interacções biofísicas em redor dos montes submarinos podem promover a agregação de presas, as quais podem atrair predadores como os cetáceos. No entanto, a interacção entre processos físicos, dinâmica das presas e o comportamento alimentar dos predadores é complexa e variável no espaço e no tempo. O objectivo principal desta tese é compreender a dinâmica da agregação de presas em redor dos montes submarinos e determinar de que forma os cetáceos exploram estas oportunidades alimentares.

Neste trabalho recorremos a campanhas de rastreio acústico para investigar a dinâmica espacio-temporal dos organismos micronectónicos (pequenos peixes epi- e mesopelágicos, cefalópodes e crustáceos) em dois montes submarinos (Condor e Gigante) dos Açores e em zonas de mar aberto. Paralelamente, foram colocados dois hidrofones para obter informação sobre a ocorrência de cetáceos nesses montes submarinos.

Os resultados demonstraram que os montes submarinos Condor e Gigante influenciam significativamente a distribuição e dinâmica do micronecton. Foram detectadas agregações substanciais no topo dos dois montes submarinos, independentemente da estação do ano e período do dia. Ao invés, a coluna de água sobre os flancos dos montes submarinos é caracterizada por concentrações de micronecton inferiores às que foram detectadas em zonas de mar aberto próximas. Enquanto no topo dos montes a comunidade de micronecton apresentava uma distribuição difusa e estava estruturada numa única camada vertical, a comunidade existente nos flancos e em mar aberto formava duas camadas distintas: uma camada de dispersão superficial (shallow-scattering layer, SSL), localizada entre a superfície e aproximadamente 150 m de profundidade, e uma camada de dispersão profunda (deep-scattering layer, DSL), dos 350 aos 650 m de profundidade. A distribuição e comportamento das duas camadas variou significativamente com a hora do dia, mas de forma inversa. Durante a noite, a densidade relativa da SSL era cerca de 5 vezes superior à registada durante o dia, a

camada apresentava-se melhor delimitada e os organismos mais densamente concentrados. No que diz respeito à DSL, a densidade diurna era o dobro da nocturna e os organismos formavam agregações mais espessas e densas durante o dia. Estes resultados sugerem que as alterações diárias nas duas camadas resultam da migração vertical nocturna e posterior agregação à SSL de parte dos organismos que compõem a DSL. Alguns destes organismos poderão ser atraídos ou passivamente transportados para a coluna de água sobre o topo dos montes submarinos, acabando por ficar retidos durante o dia. Portanto, os montes submarinos podem proporcionar enriquecido oportunidades de alimentação para os cetáceos através de uma combinação de migrações verticais e retenção local de presas.

Os resultados da acústica passiva mostraram que os delfinídeos foram detectada nos montes submarinos Condor e Gigante em praticamente todos os dias de monitorização, tendo os grupos permanecido uma média de 4 horas na vizinhança dos montes. Os sons de ecolocalização, associados ao comportamento alimentar, foram as vocalizações detectadas com maior frequência. Os dados evidenciaram um padrão diário na actividade acústica, com maior ocorrência de vocalizações durante a noite. Globalmente, os resultados deste trabalho demonstram que os pequenos delfinídeos utilizam consistentemente os montes submarinos Condor e Gigante como áreas de alimentação mas que o fazem predominantemente durante a noite.

Uma análise mais aprofundada dos padrões de distribuição de micronecton e golfinhos sugere que, à noite, os golfinhos exploram as maiores agregações de presas encontradas perto do fundo do topo do monte e/ou alimentam-se das concentrações elevadas de micronecton disponíveis nas camadas superfícies sobre os flancos dos montes submarinos, consequência da migração de organismos da DSL para a SSL. Estes resultados sugerem que a alimentação em maiores concentrações de presas mais agregadas perto do fundo do topo do monte durante o dia pode não ser energeticamente eficiente.

Este estudo contribui para uma melhor compreensão do papel dos montes submarinos na formação das comunidades micronecton em ambientes oceânicos e como isso, por sua vez, afeta a ecologia alimentar dos golfinhos.

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Chapter 1

Introduction

1. The problem: are seamounts foraging hotspots for cetaceans?

Spatial and temporal heterogeneity of physical characteristics and organisms is a general phenomenon in the ocean (Steele, 1978). The patchiness of biota can be exhibited across a broad range of scales, with distinct aggregations occurring at scales ranging from less than a meter to hundreds of kilometres and persisting from a few hours to years or even decades (Haury *et al*., 1978). Spatial and temporal patterns of organisms have profound effects on ecosystem structure and functioning by influencing species composition, population dynamics and trophic interactions, as well as the cycling of nutrients and other elements (Levin, 1992).

Small pelagic fish, cephalopods and crustaceans, that together comprise the micronekton, are the primary prey of many marine top predators. These organisms tend to aggregate over a large range of scales and the mechanisms leading to the formation and persistence of these aggregations may be a function of their life-history and biological characteristics, be linked to physical mechanisms, or result from a combination of both (Murphy *et al*., 1988; Fauchald *et al*., 2000). For example, most small pelagic fish and zooplankton live in dense schools and swarms presumably as an anti-predator response (Hamilton, 1971). The diel vertical migration behaviour that brings an immense biomass of mesopelagic fish and zooplankton to surface layers at night is also viewed as a behaviour tactic to maximize feeding success and minimize predation risk (Hays, 2003). Many fish and cephalopod species congregate seasonally to spawn in predictable regions. At meso- (10s - 1000s km) and sub-mesoscale (c. 1 km) scales, biophysical coupling at bathymetric (e.g., shelf-slopes, islands chains, seamounts) and oceanographic (e.g., fronts, eddies) features can aggregate schools of organisms into large patches (Evans, 1978). Depending on the underlying mechanism, these large patches may last for hours to months.

Aggregations of small pelagic schooling organisms are important foraging hotspots for top marine predators (Fauchald, 2009; Benoit-Bird *et al*., 2013). Predators should make optimal decisions about where to forage to maximize energy gain and, ultimately, their fitness (Stephens and Krebs, 1986). In doing so, they should seek out areas with high density of prey, and actively track concentrations of prey at different spatial and temporal scales (Curio, 1976). However, in marine pelagic systems, many spatial studies have found no or only weak aggregative response of predators towards areas of observed or expected prey concentration (see Benoit-Bird and Au, 2003a; Fauchald, 2009; Benoit-Bird *et al*., 2013).

A paradigmatic example of our inability to understand the complex spatial patterns of pelagic organisms is the case of seamount ecosystems. Seamounts represent important discontinuity structures in the open ocean that may promote a range of physical processes that can serve to concentrate prey (Genin, 2004). Upwelling, mixing and nutrient retention may enhance primary productivity, while plankton and micronekton may become entrained in convergent surface flow. Increased flow may aggregate zooplankton advected from surrounding water masses and trap their vertical migration, driving bottom-up processes across multiple trophic levels up to apex predators. This "prey aggregator" effect has often been invoked to explain the presence of pelagic predators around seamounts (see Holland and Grubbs, 2007; Kashner, 2007; Litvinov, 2007; Santos *et al*., 2007; Thompson, 2007) (Figure 1.1).

Cetaceans are highly mobile and can move over large distances at a relatively low cost and, therefore, are well adapted to exploit resources that are patchily distributed. In agreement, several studies documented the occurrence of cetaceans in areas where prey availability is expected to be higher, including hydrographic fronts, eddies, and a variety of bathymetric features (Baumgartner *et al*., 2001; Cañadas *et al*., 2002; Yen *et al*., 2004). In the case of seamounts, however, and despite anecdotal sightings, results from dedicated studies have yielded conflicting results (reviewed in Kashner, 2007) and the persistence of cetacean association to these habitats still needs to be demonstrated. This is not surprising, as most studies on seamounts are based on short-term and often coarse observations, unable to capture the spatio-temporal dynamics of both cetaceans and their prey.

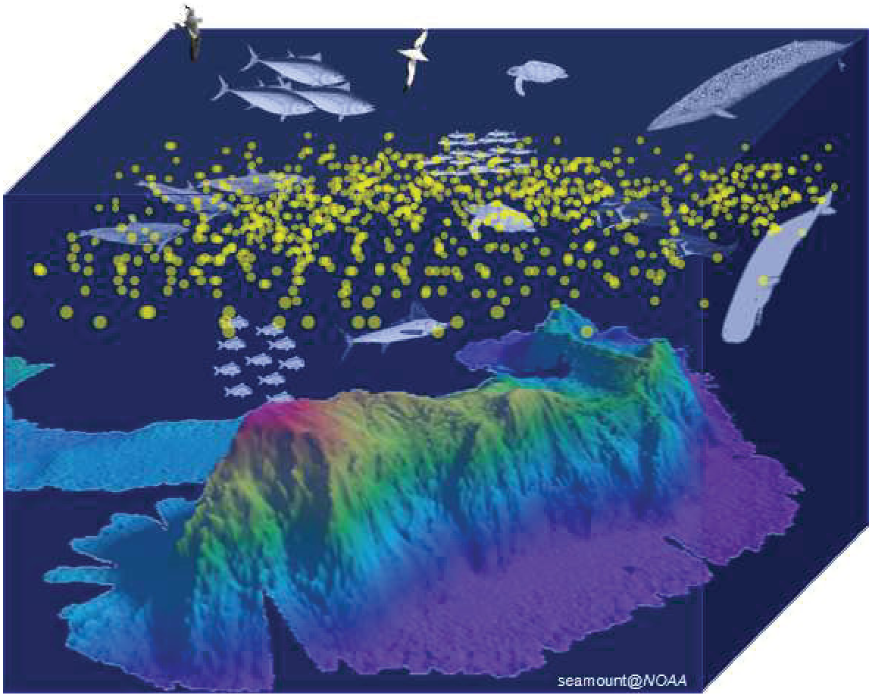

Figure 1. 1 – Seamounts as foraging hotspots for top marine predators (NOAA©).

To advance our knowledge on the effect of seamounts in predator-prey interactions, highly replicated observations of prey dynamics at fine spatial scales are critical to describe the presence and persistence of foraging hotspots at seamounts and to begin to understand the underlying behavioural and physical mechanisms. Second, long-term studies of cetaceans at seamounts, concurrent with prey information, are needed to quantify species' usage of these habitats and determine the relationship with prey dynamics. Finally, we must characterize prey in a way that is relevant for cetacean predators. Most studies use some metric of prey abundance or biomass (usually integrated over area or volume of water) to relate with cetacean distribution, disregarding the spatial scales of prey aggregation, patch density and their distribution throughout the water column. Active and passive acoustic techniques provide a great opportunity to investigate prey fields and cetacean populations at remote marine habitats.