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O PAPEL ECOLÓGICO DOS MAMÍFEROS MARINHOS

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O papel ecológico dos mamíferos marinhos

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Dedico à minha família.

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RESUMO

Os mamíferos marinhos habitam praticamente todos os oceanos do mundo, além de vários rios, estuários e mares interiores. O papel ou função ecológica de uma espécie pode ser definido como a capacidade e o grau em que ela pode influenciar outras espécies, a comunidade e o ecossistema como um todo. Nesse sentido, espécies-chave são definidas como espécies que ocorrem com uma abundância/biomassa relativamente baixa no porem exercendo uma influência estruturante no ecossistema. A investigação sobre tal função pode ser abordada por meio de duas metodologias: (*i*) o enfoque experimental ou pseudo-experimental, que consiste na avaliação dos efeitos da remoção de componentes ou perturbações causadas por motivos fortuitos no ambiente, sendo que o pré-requisito deste enfoque é o registro temporal dessas manipulações ou eventos; e (*ii*) a construção de modelos ecossistêmicos que levam em consideração diversas informações sobre as espécies, tais como distribuição, abundância, dieta, taxas metabólicas, história de vida, comportamento, dentre outras características. Nesta Tese, utilizei esta última abordagem para avaliar e aferir o papel ecológico dos mamíferos marinhos. O programa Ecopath foi o método escolhido, uma vez que ele é amplamente difundido no mundo para a exploração das características globais dos ecossistemas e de seus principais compartimentos constituintes. Entretanto, estudos de caso sobre o papel ecológico dos mamíferos marinhos baseados em informações biológicas fidedignas sobre as espécies e sobre perturbações no sistema são escassos. Além do mais, embora haja consenso entre os especialistas de que os mamíferos marinhos desempenhem um papel importante em muitos ecossistemas, a comparação do papel ecológico dos diferentes grupos de mamíferos marinhos entre diferentes tipos de ecossistemas ainda não foi avaliada de uma maneira sistemática e muitas lacunas persistem sobre como as espécies de mamíferos marinhos afetam diferentes sistemas. O objetivo principal desta tese é avaliar o papel ecológico dos mamíferos marinhos a partir de uma abordagem ecossistêmica e por meio de modelos tróficos Ecopath, dando ênfase especial na população de boto-cinza (*Sotalia guianensis*) da Baía Norte de Santa Catarina. Para tal, como primeiro passo e com o intuito maior de desvendar possíveis padrões no papel dos mamíferos em diferentes ecossistemas marinhos do mundo, foram compilados dados e meta-dados de 157 grupos funcionais de mamíferos marinhos de 55 modelos tróficos construídos no mundo e disponibilizados na plataforma Ecobase. A partir desta base de dados, formulei uma série de modelos estatísticos visando identificar e quantificar quais os fatores ou variáveis explanatórias que possam explicar melhor a variação em duas medidas complementares utilizadas para avaliar os efeitos predatórios, nomeadamente: (*i*) o índice de impacto trófico (*TI*) e (*ii*) o índice de espécie-chave (*KS*). Assim, foram selecionados os seguintes fatores: o nível trófico (*TL*), biomassa (*B*), a taxa de consumo (*QB*), o grupo taxonômico (*clade*) e a latitude aproximada onde ocorre a espécie/grupo funcional (*lat*). Os resultados deste primeiro capítulo da tese também evidenciam que $TI \sim TL$ + B * clade ($df = 9$; $logLik = 90{,}13$; $AICc = -160{,}6$; $\Delta AICc = 0$; $w_i = 0{,}444$) e $KS \sim TL + B * clade$ ($df = 9$; $logLik = 27{,}7$; $AICc = -35{,}9$; $\Delta AICc = 0{,}33$; $w_i = 0{,}245$) foram os dois modelos validados que explicavam melhor a variação das duas variáveis resposta analisadas. Conclui que não existe um padrão global no papel ecológico dos mamíferos marinhos, sendo que este é particular em cada ecossistema. Quanto superior for o nível trófico dos mamíferos marinhos, maiores serão os efeitos predatórios sobre os demais compartimentos do ecossistema sistema. Isto é por que quanto maior for o nível trófico do predador, maiores as probabilidades de ocorrerem cascatas tróficas e efeitos indiretos. Além disso, a biomassa/abundância é um fator preponderante que afeta o papel ecológico dos mamíferos marinhos, afetando tanto o impacto trófico como a posição de espécie-chave de odontocetos e pinípedes, mas não das baleias, sendo que estas podem causar um impacto maior nas suas áreas de alimentação. Assim, uma redução na biomassa de odontocetos e pinípedes poderia afetar profundamente muitos ecossistemas. Contudo, a taxa de consumo apresenta uma correlação positiva com o impacto trófico, mas isto acontece apenas com os misticetos, enquanto estes animas não apresentaram correlação com a biomassa. Os resultados sugerem ainda que, a redução nos stocks pesqueiros poderia afetar mais os mamíferos marinhos de pequeno porte devido à redução progressiva do nível trófico médio das capturas pesqueira. Adicionalmente, numa escala local, um modelo trófico Ecopath da Baía Norte de Santa Catarina, sul do Brasil, foi construído com o intuito de quantificar o papel ecológico da população mais austral do boto-cinza, avaliar o grau de vulnerabilidade desta população, além de determinar compartimentos centrais (i.e., a centralidade se refere à contribuição relativa dos compartimentos ao funcionamento do sistema, sendo que o compartimento central é aquele que apresenta a maior quantidade de energia ou matéria que entra ou sai do próprio compartimento) e discutir a interação dos botos com outros compartimentos do ecossistema, incluindo a pesca. O modelo trófico da Baía Norte de Santa Catarina mostrou ser um sistema maduro e estável, com um valor alto de *Overhead* específico ($\phi/TST = 74{,}49$ %). Com relação ao boto-cinza da Baía Norte, apresentou o maior valor de índice de espécie-chave (KS3 = 1,201) e o menor valor de Controle Sistêmico ($SCj = -28{,}57$) entre todos os grupos tróficos do modelo. Isto significa que os botos, além de terem uma função estruturante apresentando o maior impacto trófico por unidade de biomassa, é também a espécie mais vulnerável a remoção de outros compartimentos no ecossistema. Visto sua ecologia trófica de tipo oportunista/generalista e seu nível trófico superior, os botos são capazes de desencadear várias cascatas tróficas e efeitos indiretos através da teia trófica. Por fim, a corvina (*Micropogonias furnieri*), que é a principal presa dos botos além de principal espécie de peixe desembarcada pela pesca (no sentido de sua contribuição relativa de biomassa com relação à biomassa total desembarcada), foi identificada como um compartimento central do sistema. Esses resultados foram discutidos quanto à potencial aplicação na conservação da população mais austral do boto-cinza da Baía Norte de Santa Catarina, e manejo do seu ecossistema.

Palavras-chave: consumo · biomassa · mamíferos marinhos · Ecopath · nível trófico · impacto trófico · espécie-chave · boto-cinza · teia trófica · análise de redes tróficas .

ABSTRACT

Marine mammals inhabit virtually all oceans around the world, large rivers, and inshore seas as well. The ecological role of a particular species is its ability and degree to influence other species, the community, and the ecosystem as a whole. In this sense, a keystone species is a species showing a disproportionate effect on the community despite its relative low abundance/biomass. There are two possible ways in which such effects can be assessed: (i) experimental or pseudo-experimental approaches through observation and registration of likely effects of a single species' exclusion or perturbations often registered through natural experiments caused by the fortuitous removal or even the introduction of species in ecosystems, and (*ii*) modeling approaches using information on range, abundance, diet, metabolic rates, life history, behavior, and so forth. In this thesis, I used the former approach. Regarding such modeling approaches, the Ecopath framework is one of the most widely spread. Yet, case studies on the ecological role of marine mammals based on reliable information as to perturbation effects are still scarce. Moreover, although mammals are believed to play crucial role in many marine ecosystems, a systematic comparison of marine mammals' roles across different ecosystem types has not been conducted and information about the ecological role of marine mammal species is still lacking. This thesis aims to assess the ecological role of marine mammals from an ecosystem perspective using the Ecopath framework. Thus, I emphasized in the Guiana-dolphin (*Sotalia guianensis*) population that inhabits the North Bay of Santa Catarina. For that purpose, firstly, in order to explore the predatory effects of mammals in the ocean, I compiled data and meta-data of 157 marine mammal functional groups from 55 trophic models constructed throughout the world, these models featuring various ecosystem types. All models used are available from the online Ecobase repository. By using these input-output data and meta-data, I took a meta-analytical approach to unveil likely patterns regarding the predatory effects of several marine mammal groups. Aiming to identify and quantify likely factors affecting the predatory effects of marin mammal groups, I used such data-set to weight the effects of several explanatory variables on two complementay response variables, namely: (*i*) the trophic impact measure (*TI*) and (*ii*) a keystoneness index (*KS*). Namely, the explanatory variables proposed were as follows: trophic level (*TL*), biomassa (*B*), consumption rate (*QB*), taxonomic group (*clade*), and approximate latitude where the marine mammals occur (*lat*). Results from this chapter show that two validated models explained most of variation on both response variables assessed [$TI \sim TL + B * clade$ ($df = 9$, $logLik = 90.13$, $AICc = -160.6$, $\Delta AICc = 0$, $w_i = 0.444$) and $KS \sim TL$

+ B * *clade* (df = 9, *logLik* = 27.7, *AICc* = -35.9, *ΔAICc* = 0.33, w_i = 0.245)]. I concluded that there were no detectable global patterns in the trophic impact of the main marine mammal groups, nor in their keystoneness. The higher the trophic level, the greater the trophic impact of marine mammals. This is because the higher the trophic impact, the greater the probabilities for both trophic cascades and indirect effects to occur. Furthermore, increasing the biomass/abundance can increase the predatory effects on the trophic impact and keystoneness of odontocetes and pinnipeds, but greater in the former group. However, biomass variation showed no effects on the predatory effects of baleen whales, even though consumption rate variations showed a positive effect on the trophic impact of mysticetes. This means that declines in the abundance of odontocetes can cause significant changes in many marine ecosystem, while the impact of baleen whales could be greater in their feeding grounds through increasing their consumption rates. Also, my results suggest that, given their higher trophic levels, odontocetes and pinnipeds can be more vulnerable to the fishing down marine food web effect, which is gradual transition in landings from long-lived, high trophic level, piscivorous bottom fish toward short-lived, low trophic level invertebrates and planktivorous pelagic fish. Regarding to the second chapter of this thesis, I constructed an Ecopath food web model of the North Bay ecosystem in order to stress the predatory effects and keystoneness of the southernmost population of the Guiana-dolphin. My findings showed the North Bay ecosystem is a mature, detritus-based and stable ecosystem (ϕ/TST = 74.49 %). By stressing the predatory effects of the Guiana-dolphins, I show how dolphins may be beneficial to other compartments and to the ecosystem as a whole because they a keystone species, as they showed the highest *KS3* keystoneness index score (*KS3* = 1.201) among all compartments in the ecosystem, which means the species is a keystone species in the North Bay food web. I also described how this species links to other compartments in the food web. Given the dolphins' high trophic level and opportunistic feeding ecology, this compartment can trigger several trophic cascades and indirect effects throughout the food web. Beside the dolphins' predatory effects, the dolphins may be most vulnerable to perturbations, given that they showed the lowest estimated Systemic Control (SC_j = -28.57). In other words, although a keystone species, they are vulnerable. I also was able to identify the central species in the food web (throughflow centrality indicates species functional importance in ecosystems since such species have the greatest amount of energy-matter entering or exiting the component itself). The whitemouth croaker (*Micropogonias furnieri*) is a hub species in the North Bay food web (T_j = 1000364 t * km^2 * year^{-1}). Such fish species is the main prey for the dolphins and an important fish landed by the fishery. I discussed how the results of my thesis can be

taken intoconsideration to face management and conduct conservation policies in order to protect the southernmost population of the Guiana-dolphin inhabiting the North Bay's ecosystem.

Keywords: consumption · marine mammal · Ecopath · trophic level · trophic impact · keystoneness · Guiana-dolphin · food web · ecological network analysis .

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LISTA DE ABREVIATURAS E SIGLAS

AIC	Akaike Information Criteria
B	Biomassa
CAPES	Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
EE	Eficiência Ecotrófica
ENA	Ecological Network Analysis
EwE	Ecopath with Ecosim
KS	*Keystone species*
MTI	*Mixed Trophic Impact*
QB ou Q/B	Taxa de Consumo
PB ou P/B	Taxa de Produção
PMAP-SC	Programa de Monitoramento da Atividade Pesqueira de Santa Catarina
TI	Impacto trófico relativo
TL	*Trophic Level*

SUMÁRIO

APRESENTAÇÃO

A interação entre os mamíferos marinhos e o ecossistema no qual eles habitam, e como eles interagem com os demais componentes da teia trófica, pode ser abordada de dois modos possíveis: podemos abordar os efeitos do ecossistema sobre os mamíferos marinhos como podemos abordar os efeitos dos mamíferos marinhos sobre o ecossistema. Esta Tese procurou analisar esta interação principalmente usando a segunda abordagem mencionada anteriormente. Sendo assim, o papel ou função ecológica dos mamíferos marinhos foi definido como a capacidade de eles influenciarem outras espécies da comunidade e dentro do ecossistema (Estes et al. 2016). Entretanto, é preciso salientar que, para além desta abordagem principal, alguns dos resultados possibilitaram desvendar efeitos prejudiciais de outros componentes sobre os mamíferos marinhos e até mesmo fazer uma avaliação da vulnerabilidade de uma população muito particular de boto-cinza (*Sotalia guianensis*): a população residente na Baía Norte de Santa Catarina, sendo que esta localidade representa o extremo sul de distribuição da espécie (Simões-Lopes 1988).

A estruturação desta tese consiste em uma introdução geral seguida de dois capítulos. Na introdução é possível identificar três seções. Na primeira seção da introdução, embora de um modo sucinto, pretende-se apresentar os mamíferos marinhos de forma cabal, enfatizando aspectos relevantes sobre a distribuição, adaptações, a alimentação e ecologia trófica dos principais grupos. Na segunda seção da introdução foram definidos alguns conceitos da Ecologia que são importantes para entender as premissas e os objetivos desta Tese. Na terceira e última seção da introdução, há um detalhamento das questões relacionadas à modelagem ecológica utilizando o programa Ecopath e questões ecológicas implementadas no próprio programa. Em seguida, os dois capítulos constituintes da Tese são apresentados.

O primeiro capítulo aborda o papel ecológico dos mamíferos marinhos em diferentes ecossistemas do mundo e apresenta uma série de meta-análises (envolvendo parâmetros básicos, "outputs" e meta-dados) com o intuito de explorar possíveis padrões no papel ecológico dos principais grupos de mamíferos marinhos em diferentes ecossistemas, além de desvendar fatores que podem influenciar os efeitos predatórios destes animais nos ecossistemas. No segundo capítulo, a estrutura e o funcionamento do ecossistema da Baía Norte de Santa Catarina foram descritos por meio da construção de um modelo trófico Ecopath, objetivando explorar o papel ecológico do boto-cinza (*Sotalia guianensis*) residente neste ecossistema por meio da utilização de indicadores ecossistêmicos implementados no Ecopath, mas também por meio da análise de redes tróficas.

INTRODUÇÃO

OS MAMÍFEROS MARINHOS NO MUNDO

Os mamíferos marinhos, como os mamíferos terrestres, pertencem à classe Mammalia, que inclui mais de 6000 espécies em 25 ordens (Burgin et al. 2018). Os mamíferos marinhos são aqueles que vivem toda ou parte da sua vida no mar. Embora muitos habitem todos os oceanos do mundo, outros habitam rios caudalosos, estuários e mares interiores. Apesar das espécies de mamíferos de água doce não serem marinhas no sentido estrito, o parentesco com as espécies marinhas é muito próximo, e por causa disso, nesta Tese ambos os termos (ou seja, mamíferos marinhos e mamíferos aquáticos) são considerados indistintamente, sendo que é mais frequentemente usada a expressão "mamíferos marinhos" de modo genérico ao longo desta Tese. Há em torno de 120 espécies viventes de mamíferos marinhos (The Society for Marine Mammology 2021), sendo que algumas espécies permanecem a vida toda no ambiente aquático, enquanto outras espécies passam a maior parte da vida neste ambiente.

Os mamíferos marinhos viventes incluem uma assembleia diversificada de espécies com representantes de três ordens de mamíferos. Dentro da ordem **Carnivora** há os pinípedes (focas, lobos marinhos, morsas), a lontra marinha e o urso-polar. Dentro da ordem **Cetacea** há baleias, cachalotes, orcas, delfins, e toninhas. Já dentro da ordem **Sirenia** há o peixe-boi. Os mamíferos aquáticos ou marinhos foram mais diversificados no passado, já que existiram grupos atualmente extintos tais como os desmostílios, tendo sido este um animal parecido com os hipopótamos, além do *Kolponomos*, um bizarro animal parecido com um urso de grande porte, e até mesmo o bicho-preguiça-marinho *Thalassocnus*. Existem evidências que todos os mamíferos marinhos evoluíram em diferentes episódios a partir de ancestrais terrestres. Atualmente só podemos especular sobre as razões que moveram os mamíferos terrestres a colonizarem o ambiente marinho e a sua evolução posterior para espécies que passam toda ou parte da sua vida no mar. Certamente, aqueles ancestrais procuravam tirar um maior proveito de vastos e novos recursos alimentares oferecidos pelo mar. Assim, a definição dos mamíferos marinhos enquanto grupo responde mais a convergências evolutivas do que às relações filogenéticas entre eles (Reynolds et al. 1999, Berta et al. 2005).

Os mamíferos marinhos são organismos endotérmicos que geram e regulam sua temperatura interna e corporal entorno aos 37 °C por meio da variação das suas taxas metabólicas, além de eles viverem a maior parte da vida, se não toda, em um ambiente líquido significativamente mais frio, o que significa que para eles a vida é um desafio térmico considerável (Castellini 2009). Existe, porém, variação no grau de adaptação das espécies. Enquanto alguns grupos como os pinípedes, as lontras e os ursos-polares precisam alocar tempo em terra firme para acasalarem e mudarem a pele, os cetáceos e os sirênios são completamente aquáticos. Dentre as várias adaptações, podemos mencionar a da pele (principalmente da hipoderme ou tecido subcutâneo), sendo que estes animais desenvolveram uma camada espessa de tecido adiposo vascularizado que funciona como vedação térmica, enquanto algumas espécies também desenvolveram uma grossa pelagem. Além disso, pode-se mencionar adaptações metabólicas, como o fato de os mamíferos marinhos apresentarem taxas metabólicas elevadas, sendo que estas adaptações possibilitaram a vida destes mamíferos no ambiente aquático, uma vez que taxas metabólicas elevadas podem contrarrestar a perda de calor por condução ou difusão térmica entre o organismo e o ambiente. É interessante mencionar aqui que a possível correlação entre variações nas taxas metabólicas e a função ecológica dos mamíferos marinhos já foi levantada anteriormente por outros pesquisadores (Morissette & Brodie 2015). Contudo, embora os diferentes grupos taxonômicos de mamíferos marinhos difiram na origem filogenética, todos eles apresentam as adaptações análogas ao ambiente marinho.

Com relação à distribuição, os mamíferos marinhos podem ser considerados animais bem-sucedidos, tendo sido capazes de conquistar diversos habitats. Algumas espécies, como delfins de rio e a foca-monge-do-Havaí (*Monachus schauinslandi*), apresentam uma distribuição muito restrita (embora a distribuição da foca-monge-do-Havaí já tenha sido maior no passado). Outras como a baleia-jubarte (*Megaptera novaeangliae*) e os cachalotes (*Physeter macrocephalus*) ocorrem no mundo inteiro. Em geral, a distribuição das espécies está associada com a distribuição dos recursos alimentares dos quais cada espécie depende, sendo que estes recursos podem variar sazonalmente. No entanto, com exceção do urso-polar (*Ursus maritimus*), o peixe-boi-da-amazônia (*Trichechus inunguis*) e algumas espécies de baleias, os mamíferos marinhos normalmente precisam se alimentar durante o ano todo. Nesse último caso, a própria distribuição da espécie está correlacionada com a distribuição dos recursos alimentares (Reeves et al. 2002). Embora, os mamíferos aquáticos habitem uma ampla gama de condições ambientais, incluindo regiões tropicais, regiões polares, corpos d’água doce, corpos d’água salgada e/ou saloba, eles não habitam as profundezas abissais dos oceanos. Contudo, os elefantes-marinhos (*Mirounga* spp.), os cachalotes (*Physeter macrocephalus*), e outras várias espécies são capazes de mergulhar com destreza até profundidades maiores que 1000 m, onde é frio e escuro e com pressão 100 vezes maior que a pressão atmosférica (Würsig 2009).

Algumas espécies apresentam distribuição muito restrita. Por exemplo, alguns botos ocorrem exclusivamente em rios. Além dos botos, o peixe-boi-da-Amazônia habita o rio Amazonas e seus tributários, sempre confinado na água doce, sem ter contato com água salgada. A foca-do-mar-Cáspio (*Pusa caspica*) e o nerpa ou foca-de-Baikal (*Pusa sibirica*) ocorrem apenas dentro destes dois corpos d'água. No entanto, outras espécies apresentam distribuição bem mais abrangente, embora às vezes confinada dentro de um hemisfério ou bacia específica. A baleia-da-Groenlândia (*Balaena mysticetus*) ocorre apenas nas águas do Ártico e a baleia-cinzenta (*Eschrichtius robustus*) e a lontra-marinha (*Enhydra lutris*) habitam exclusivamente o nordeste do Pacífico. Nenhuma espécie de pinípede ocorre em ambos os hemisférios, já algumas espécies de baleias se distribuem para o norte ou para o sul do Equador, mas nunca para ambos os hemisférios. Por exemplo, a distribuição da baleia-cinzenta (*Eschrichtius robustus*) abrange exclusivamente algumas regiões do hemisfério Norte (Jefferson et al. 2011), enquanto a baleia-minke-austral (*Balaenoptera bonaerensis*) habita apenas o hemisfério Sul (Bastida & Rodríguez 2003).

Muitas espécies de baleias de grande porte são cosmopolitas. Por exemplo, a baleia-jubarte ocorre em todos os oceanos do mundo e em diferentes épocas do ano tanto nas regiões tropicais como nas regiões polares. Além desta espécie, muitas espécies ocorrem em ambos os hemisférios, tais como baleias-azuis (*Balaenoptera musculus*), baleias-fin (Balaenoptera physalus), baleia-sei (*Balaenoptera borealis*) e as baleias-de-Bryde (*Balaenoptera brydei* e *Balaenoptera edeni*) usam ambos hemisférios. O termo circumpolar é usado para se referir à distribuição de uma espécie que ocorre próxima a um dos polos. Uma espécie que ocorre em águas tropicais para ambos os lados do Equador é uma espécie de distribuição pan-tropical. As espécies que apresentam um tipo de distribuição costeira ocorrem sempre próximas da costa, e frequentemente também em estuários, golfos, baías e enseadas. Muitas espécies de mamíferos marinhos apresentam distribuição costeira. Muitas espécies de delfins como o boto-cinza (*Sotalia guianensis*) e a toninha (*Pontoporia blainvillei*) e pinípedes como o lobo-marinho-sul-americano (*Arctocephalus australis*) apresentam este tipo de distribuição, que não é tão comum entre as baleias. Outras espécies apresentam um tipo de distribuição pelágica ou oceânica. Por exemplo, os cachalotes são uma espécie de distribuição pelágica restrita, sendo uma raridade a sua aproximação da costa, exceto no caso daquelas regiões onde a plataforma continental é estreita e o talude continental fica próximo da costa e há águas profundas por perto do litoral. Por outro lado, enquanto a maioria das baleias-jubarte realizam extensas migrações sazonais entre as latitudes altas e baixas, existe uma população desta espécie que habita permanentemente as águas quentes do mar Arábico (Reeves et al. 2002).

Entretanto, dentro de uma espécie dada, variações notáveis nos padrões de distribuição entre populações não são incomuns. Por exemplo, há várias populações de golfinho-nariz-de-garrafa (*Tursiops truncatus*) que habitam diferentes tipos de hábitats, sendo que algumas populações ocorrem em águas oceânicas, outras em ambientes costeiros e inclusive estuarinos. Contudo, estudos recentes mostraram que há diferenciação trófica dentro da espécie (Pereira et al. 2020), sendo que o ecótipo costeiro *Tursiops truncatus gephyreus*, derivou a partir do ecótipo oceânico, *Tursiops truncatus truncatus* (Costa et al. 2021). Assim, a especialização na exploração de recursos e preferências alimentares pode ser uma força de seleção importante no processo de especiação dos mamíferos marinhos.

Além da variação na abundância e distribuição de espécies, existe variação significativa tanto na composição da dieta como na ecologia trófica dos mamíferos marinhos (Barros & Clarke 2009). Enquanto grupo, a evolução dos mamíferos marinhos fez com que estes animais se adaptassem a explorar um leque surpreendente de espécies de presas, havendo grande variação no nível trófico das espécies de mamíferos marinhos. Em um dos extremos, as baleias representam um dos maiores paradoxos do mundo natural, sendo que neste caso os maiores animais do planeta subsistem do consumo de alguns dos menores organismos vivos. As baleias-francas (*Eubalaena* spp.) se alimentam exclusivamente de organismos zooplanctônicos, sendo que isto é por sua vez prova da extraordinária produtividade do mar. De maneira similar, a baleia-azul (*Balaenoptera musculus*), que é o maior animal que já viveu no planeta, alimenta-se de pequenos crustáceos semelhantes ao camarão chamados de krill (eufausídeos). Outras espécies de baleias, como por exemplo, a baleia-sei ou rorqual-sardinheiro (*Balaenoptera borealis*) e a baleia-comum (*Balaenoptera physalus*) também se alimentam principalmente de krill. No outro extremo, a orca (*Orcinus orca*) é um predador voraz cuja dieta pode incluir peixes enormes e velozes como o atum-rabilho (*Thunnus thynnus*), além de focas, delfins e inclusive mamíferos marinhos de porte maior. De fato, as orcas às vezes são bem-sucedidas na predação sobre algumas espécies de cetáceos de grande porte, inclusive baleias-azuis e cachalotes (Reeves et al. 2002).

Ao longo da evolução as baleias desenvolveram barbatanas que possibilitam o aproveitamento e consumo dos recursos mais abundantes do mar. Enquanto algumas espécies mostram uma composição de dieta diversificada, outras espécies especializam sua alimentação a um leque limitado de presas. Por exemplo, a baleia-jubarte (*Megaptera* *novaeangliae*) se alimenta de krill e várias espécies de peixes pelágico que formam cardumes. Já a baleia-azul se alimenta quase exclusivamente de krill. Espécies especialistas no forrageio são chamadas de estenófagas. Assim, podemos dizer que a baleia-azul é estenófaga no krill (Reeves et al. 2002). Pivorunas (1979) classificou as baleias em três grandes grupos tróficos: (*i*) os rorquais ou balenopterídeos, que se alimentam principalmente de cardumes de peixes e de crustáceos como o krill, sendo que dentro deste grupo há espécies tais como a baleia-comum (*Balaenoptera physalus*), o rorqual-sardinheiro (*Balaenoptera borealis*), o rorqual-de-Bryde (*Balaenoptera brydei*), o rorqual-de-Bryde-anão (*Balaenoptera edeni*), a baleia-azul (*Balaenoptera musculus*), o rorqual-anão-boreal (*Balaenoptera acutorostrata*), o rorqual-anão-austral (*Balaenoptera bonaerensis*), a baleia-de-Omura (*Balaenoptera omurai*) e a baleia-jubarte (*Megaptera novaeangliae*); (*ii*) outro grupo inclui as baleias-francas, que se alimentam preferencialmente de copépodes, sendo que este grupo inclui espécies como a baleia-franca-austral (*Eubalaena australis*), a baleia-franca-do-Atlântico-norte (*Eubalaena borealis*), a baleia-franca-do-Pacífico (*Eubalaena japonica*) e a baleia-da-Groenlândia (*Balaena mysticetus*); e (*iii*) a baleia-cinzenta (*Eschrichtius robustus*), que forrageia organismos bentônicos no fundo do mar em águas pouco profundas do hemisfério Norte, sendo que se estima que a espécies pode remover entre 9 e 27% do bentos cada ano no ecossistema do norte do Mar de Bering (Nerini 1984), cumprindo um papel ecológico crucial por meio da reestruturação física das comunidades bênticas (Bowen 1997). Porém, cabe esclarecer que estudos mais recentes mostram que, no caso da baleia-franca-austral, a composição da dieta pode variar de uma área de alimentação para outra (Valenzuela et al. 2018), indicando que a disponibilidade de presas pode ter uma influência maior que as adaptações e/ou preferências na dieta das baleias-francas.

Via de regra, as presas dos odontocetos são de porte maior que as dos misticetos (Jefferson et al. 2009). Odontocetos normalmente predam sobre peixes de tamanhos variados, incluindo espécies pequenas como arenques e peixes da família Ammodytidae, espécies de tamanho médio como o bacalhau, o salmão e o linguado, e espécies de grande porte como o atum e os tubarões. Os cefalópodes, especialmente as lulas, constituem a principal presa de muitas espécies de odontocetos, como no caso dos cachalotes, as baleias-piloto (*Globicephala* spp.) e os zífios ou baleias-bicudas (família Ziphiidae). Algumas populações de orcas (*Orcinus orca*) se alimentam principalmente de mamíferos marinhos como focas, lobos marinhos e cetáceos, mas também de aves como os pinguins. Embora a observação direta de eventos predatórios de orcas sobre cefalópodes e peixes (incluindo tubarões) seja rara e metodologicamente difícil de fazer, existem evidências que confirmam que as orcas também podem consumir estas duas últimas categorias de presa mencionadas (Higdon et al. 2013), sendo que o tipo de presa consumido parece estar mais associado à disponibilidade de recursos alimentares do que à especialização, embora essas duas possibilidades não são mutuamente excludentes (Lefort et al. 2020).

Os odontocetos se alimentam em profundidades variáveis. Enquanto delfins e marsuínos (também chamados de porcos-marinhos, referindo-se às espécies da família Phocoenidae) se alimentam em águas relativamente próximas da superfície, baleias-bicudas e cachalotes normalmente caçam em profundidades de até centenas de metros. Embora muitos pinípedes se alimentem próximos da superfície, algumas espécies de focídeos de porte maior podem mergulhar a grandes profundidades para buscar seu alimento, tal como é característico na foca-de-Weddell (*Leptonychotes weddellii*) e nos leões-marinhos (família Otariidae). Esta capacidade de mergulhar a grandes profundidades parece estar influenciada por algumas características comportamentais, sendo que há evidências que provam que o mergulho planado da foca-de-weddell reduz entre 9.2 e 59.6% o gasto energético do animal (Williams et al. 2000).

Diferentemente das baleias, que normalmente tragam grandes porções de alimento ingerindo milhares e até milhões de organismos de uma vez só, os odontocetos normalmente se alimentam engolindo um item (como um indivíduo de peixe) de cada vez. Normalmente eles engolem a presa inteira, com os dentes cumprindo a função de segurar ao invés de mastigar. É provável que a sucção cumpra uma importante função na hora de capturar as presas para muitos odontocetos (Werth 2006).

Semelhante aos odontocetos, os pinípedes são exímios caçadores, podendo se alimentar de diversas espécies de peixes, incluindo peixes grandes como bacalhaus e salmões, lulas, além de outros tipos de presa. Embora a morsa (*Odobenus rosmarus*) se alimente principalmente de moluscos, é conhecido que também predam sobre peixes e que alguns indivíduos “trapaceiros” matam e comem outros pinípedes. Quiçá o mais voraz dos pinípedes seja a foca-leopardo (*Hydrurga leptonyx*) que é capaz de atacar qualquer presa que estiver disponível, ora krill e lulas, ora pinguins e outras espécies de pinípedes. Assim, os pinípedes se alimentam nos mesmos níveis tróficos que os odontocetos, com exceção das orcas (*Orcinus orca*) que se alimentam em níveis tróficos superiores (Pauly et al. 1998).

Dentre as presas das lontras, que variam de uma população para outra, podemos mencionar moluscos, ouriços, crustáceos e peixes. As lontras marinhas forrageiam em águas costeiras e, apesar de elas serem consideradas generalistas, individualmente a dieta costuma ser pouco diversificada. As lontras (*Enhydra lutris*) normalmente apanham suas presas no fundo do mar e utilizam uma pedra para quebrar as conchas dos moluscos, os quais consomem na superfície (Marshall 2009). Estudos realizados nas costas sudestes do Alaska mostram que a dieta das lontras (*Enhydra lutris*) tende à especialização no consumo da amêijoa-manteiga (*Saxidomus giganteus*) e que a presença de toxinas nestes organismos pode ser um fator importante na distribuição das lontras (Kvitek et al. 1993).

Por fim, o urso-polar (*Ursus maritimus*) pode se alimentar de espécies de peixes e às vezes até mesmo de belugas (*Delphinapterus leucas*) e narvais (*Monodon monoceros*), embora sua dieta seja predominantemente baseada na foca-anelada (*Pusa hispida*, também nomeada como *Phoca hispida*), e em menor frequência na foca-barbuda (*Erignathus barbatus*) e várias espécies de aves marinhas. Análises de conteúdos estomacais com técnicas tradicionais de identificação de estruturas duras combinadas com análises genéticas de material fecal podem fornecer uma melhor compreensão e ponderação da dieta dos ursos-polares, além de complementar o conhecimento obtido a partir de estudos observacionais do comportamento predatório destes animais (Iversen et al. 2013).

O comportamento de forrageio dos mamíferos marinhos é quase tão diversificado quanto o tipo de presas que eles consomem. Enquanto os sirênios simplesmente pastejam (e às vezes podam) na vegetação, os demais mamíferos marinhos utilizam os sentidos e direcionam seu comportamento para buscarem o alimento. Provavelmente todos os odontocetos possuem algum sonar biológico, chamado de ecolocalização, que eles utilizam tipicamente para buscarem suas presas. Questões comportamentais são importantes fatores determinantes do papel ecológico dos mamíferos marinhos. Por exemplo, algumas tácticas de forrageio dos mamíferos marinhos podem facilitar o forrageio para outras espécies, como para as aves marinhas, sendo que este efeito benéfico pode fazer com que duas redes tróficas em ambientes diferentes fiquem interligadas (Kiszka et al. 2015). No entanto, a quantificação da natureza e magnitude de tal facilitação ainda seja um assunto que deve ser investigado de uma maneira mais aprofundada.

Como os pinípedes, as lontras costumam se alimentar próximos da superfície. É interessante mencionar que os mamíferos marinhos de pequeno porte podem ser predados por mamíferos marinhos de porte maior, sendo que a combinação dos efeitos predatórios das espécies de mamíferos marinhos em um dado ecossistema pode ter efeitos ecossistêmicos significativos. Como exemplo paradigmático, podemos mencionar a modificação do habitat desencadeado pelo disparo de cascatas tróficas causado pela mudança nos hábitos alimentares das orcas (*Orcinus orca*) sobre as lontras (*Enhydra lutris*) nas costas do nordeste do Pacífico (Estes et al. 1998), sendo que uma menor pressão predatória das orcas sobre as lontras pode acarretar mudanças profundas nas florestas subaquáticas de kelp, com a consequente alteração do ecossistema como um todo (Roemer et al. 2009).

Dentre as técnicas de caçada mais interessantes que os mamíferos marinhos utilizam, podemos mencionar o borbulhar usado pelas baleias-jubarte para pegar peixes, sendo que com frequência este esforço pode ser feito coletivamente. Em algumas espécies, o forrageio cooperativo está bem desenvolvido. As orcas, por exemplo, são caçadores proficientes quando em grupo (Pitman & Durban 2012), sendo que frequentemente trabalham juntas para cercar e capturar peixes e mamíferos marinhos. As baleias geralmente se alimentam sozinhas, mas em alguns casos, como nas baleias-jubarte (*Megaptera novaeangliae*), os animais trabalham juntos para explorar cardumes de peixes (Mastick 2016). Pelo contrário, pinípedes, lontras, e ursos-polares são geralmente predadores solitários. Existem também alguns casos bem documentados de pesca cooperativa entre humanos e cetáceos. Por exemplo, a população de *Tursiops truncatus gephyreus* em Laguna, no litoral sul do Brasil, apresenta uma peculiaridade comportamental. Alguns indivíduos desenvolveram a habilidade de interagir com pescadores artesanais durante a captura de tainhas (*Mugil* spp.). Esta interação, estereotipada e sincronizada, aparentemente gera benefício mútuo, facilitando o acesso à presa (Simões-Lopes 1991, Simões-Lopes et al. 1998, Daura-Jorge et al. 2013).

PREDAÇÃO E ECOLOGIA TRÓFICA

A influência que uma espécie pode exercer sobre as demais espécies que compõem o ecossistema pode ser categorizada como positiva, negativa ou neutra (Ulanowicz & Puccia 1990). Visto que o consumo resultante da relação predador e presa entre duas espécies é possivelmente a forma mais preponderante de interação entre espécies, e considerando que os predadores são, via de regra, sustentados energeticamente por suas presas, a natureza da influência de uma presa sobre seu predador é quase sempre positiva. Da mesma forma, visto que as presas são normalmente abatidas ou depredadas pelos seus predadores, a influência de um predador sobre a sua presa costuma ser negativo.

Além disso, as interações entre um predador e sua presa podem ser fracas ou fortes, além de elas poderem ser simétricas ou assimétricas. Por exemplo, como um caso especial de interação trófica entre dois componentes no contexto de uma teia trófica, um tipo de mutualismo pode ser definido quando ocorre a situação em que ambos os efeitos de um componente sobre o outro são reciprocamente positivas (Estes 2009). Atualmente, além do crescente interesse pelo estudo do papel ecológico das espécies (Bornatowski et al. 2016, Pan et al. 2016), há vastas evidências de que muitas espécies de vertebrados de grande porte, possam exercer um papel crucial em muitos ecossistemas aquáticos (Pace et al. 1999, Shurin et al. 2002). Se os mamíferos marinhos fossem de fato modeladores da estrutura e funcionamento de muitos ecossistemas, mudanças na abundância deles poderiam causar efeitos ecológicos notáveis em muitos ecossistemas. Portanto, pode-se afirmar que a futura estrutura e funcionamento de muitos ecossistemas dependem da distribuição e abundância presentes dos mamíferos marinhos, das suas dinâmicas populacionais, mas também do tipo de manejo adotado (Estes 2009).

As cascatas tróficas podem ser definidas como aqueles efeitos indiretos que afetam a abundância, a biomassa ou a produtividade de uma população, uma comunidade ou até mesmo um nível trófico através de mais de uma conexão (ou seja, mais de uma relação de predador e presa) no ecossistema. Sendo assim, cascatas tróficas são fortes interações que ocorrem dentro de uma teia trófica e que afeta as propriedades do sistema como um todo. Algumas espécies exercem efeitos predatórios estruturantes numa teia trófica ao estabilizar o ecossistema em um ‘estado-alternativo’, sendo que a análise da exclusão es espécies de animais de grande porte pode causar perda de cascatas tróficas, afetando o ecossistema e impedindo a recuperação de vários componentes de ecossistemas disturbados (Pace et al. 1999). Aliás, há evidências contundentes sobre a existência destes estados-alternativos nos ecossistemas, nos quais a natureza das interações e a composição e abundância de espécies podem variar substancialmente de um estado para o outro (Scheffer et al. 2001). Visto que as populações de mamíferos marinhos têm sido historicamente submetidas a fortíssimas pressões induzidas por atividades humanas, pode-se esperar que tanto a recuperação das populações de mamíferos marinhos como aquelas mudanças resultantes do manejo alterem significativamente a configuração da teia trófica (estrutura) e o regime de fluxo de matéria e energia (funcionamento) nos ecossistemas.

Como exemplo paradigmático de cascata trófica há a interação entre a lontra (*Enhydra lutris*), os ouriços (*Strongylocentrotus franciscanus*), e as algas (kelp) na costa oeste da América do Norte (Estes & Duggins 1995). Ao exercerem pressão predatória sobre os ouriços consumidores de algas (kelp), as lontras estabilizam um sistema onde as florestas subaquáticas de kelp podem se desenvolver e conseguem se tornar abundantes. A remoção da lontra provoca alterações no sistema que fazem com que os ouriços se tornem dominantes, provocando uma redução substancial tanto na cobertura quanto na produtividade das algas (kelp). Este é um exemplo de interação indireta através de uma teia trófica, sendo que o contraste entre esses dois possíveis 'estados-alternativos' pode ser considerável. Portanto, cascatas tróficas podem provocar mudanças dramáticas tanto na aparência como nas propriedades do ecossistema.

O caso da lontra da Costa Oeste da América do Norte é um caso paradigmático de cascata trófica no qual a interação ocorre de um modo linear e direcionado conforme um fluxo de matéria e energia bem estabelecido, como acontece no caso de uma cadeia trófica (Fig 1a). Contudo, dentro de uma teia trófica, enquanto o fluxo de matéria e energia nem sempre é linear ou direcionado, outros tipos de interações tróficas podem acontecer. Por exemplo, a competição entre dois predadores de topo por uma determinada presa (Fig 1b). Além desta última interação, também podem ocorrer casos de interações indiretas bem mais complexas (Fig 1c). Em outras palavras, se A influencia C, e C interage com B, logo uma via indireta existe entre A e B. Este último tipo de interação trófica pode causar efeitos significativos e surpreendentes dentro de uma teia trófica (Ulanowicz & Puccia 1990, Abrams et al. 1996, Yodzis 2001). Com relação aos efeitos de uma espécie sobre si mesma, eles são normalmente negativos por conta da competição intra-específica. Entretanto, há casos em que um acréscimo do *stock* de uma espécie dada pode ser benéfica para a própria espécie. Por exemplo, no caso do circuito auto-catalítico ("*autocatalytic loop*" em Inglês) uma espécie A produz os recursos necessários para a espécie B, enquanto a espécie B produz os recursos necessários para C, e por fim a espécie C produz os recursos necessários para a espécie A (Veldhuis et al. 2018).

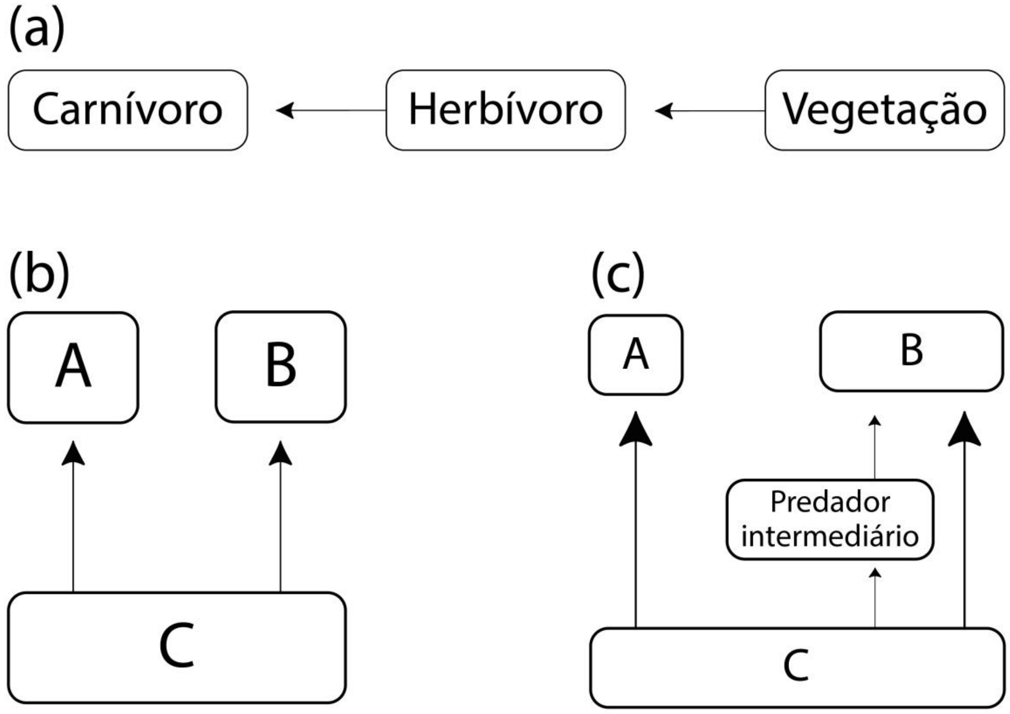

Figura 1. O gráfico esquematiza três tipos de interações tróficas que podem ocorrer em um ecossistema e desencadear diferentes efeitos nas populações dos componentes, comunidades e no ecossistema como um todo. (a) representa um clássico exemplo de cascata trófica, onde um aumento da abundância do predador (Carnívoro) pode provocar como efeito uma diminuição na abundância da sua presa (Herbívoro), sendo que este efeito pode ser repassado ao nível trófico inferior (Vegetação), causando um maior desenvolvimento deste em função à exclusão dos seus forrageadores. (b) representa um exemplo de competição, onde um aumento da população do predador (B) pode provocar como efeito uma diminuição na abundância da presa (C), prejudicando ao outro predador (A). Por fim, a figura (c) representa um exemplo de interação indireta, onde dependendo da intensidade das interações tróficas entre os componentes envolvidos, embora uma possível diminuição na população do predador B possa acarretar um aumento na população da presa (C) como efeito direto, ela também pode favorecer um aumento da população do predador intermediário, que na sua vez pode provocar uma diminuição na população da presa (C), o que pode acabar prejudicando ao predador A. A representação gráfica desta figura foi adaptada a partir de Yodzis (2001).

Assim, a tarefa de desvendar as interações tróficas entre os componentes de um ecossistema e o grau em que cada um destes componentes influencia o ecossistema como um todo e os demais componentes continua a ser um grande desafio visando a predição de dinâmicas ecológicas e o manejo de ecossistemas. Logo, é possível que a remoção ou redução na presença e abundância dos mamíferos marinhos nos mares do mundo possa acarretar uma perda de cascatas tróficas prejudicando assim o ambiente e o ecossistema (Pace et al. 1999). É possível que em alguns casos, essa perda também tenha o potencial de prejudicar muitas atividades humanas, tais como a pesca (Yodzis 2001).

Neste contexto, compreender o papel ecológico dos mamíferos marinhos é um desafio e uma das principais questões da ecologia marinha. Como uma das possíveis abordagens, pode-se registrar e documentar as possíveis mudanças que possam estar acontecendo no ambiente perante a decorrente recuperação/declínio das populações de mamíferos marinhos nos mares do mundo. Outra abordagem recomendável é a modelagem ecológica envolvendo características demográficas, comportamentais e a bioenergética (Estes et al. 2016). Embora esta última abordagem não ofereça uma resposta categórica sobre os possíveis efeitos dos mamíferos marinhos sobre o ecossistema perante as mudanças ambientais, ela certamente possibilita a formulação de hipóteses sobre quais podem ser tais efeitos, sendo esta uma parte essencial no processo.

A compreensão da natureza e força das interações entre espécies é chave tanto para o desenvolvimento de modelos preditivos de redes tróficas naturais como para o desenvolvimento de estratégias de conservação e manejo (Berlow et al. 1999). Adicionalmente, ao investigar a natureza e força das interações entre espécies numa teia trófica e o papel ecológico das espécies, vem à tona a identificação de espécies-chave (ver seção 1.3.4 desta Tese). Uma espécie-chave é uma espécie com uma abundância/biomassa relativamente baixa que cumpre um papel preponderante na estruturação da teia trófica (Libralato et al. 2006, Heithaus et al. 2008). Assim, a identificação de espécies-chaves no contexto da teia trófica é crucial para a conservação e o manejo ecossistêmico (Jordan 2009).

Em síntese, em termos de manejo, há razões para acreditar que é tão importante proteger uma espécie-chave quanto uma espécie rara ou ameaçada, uma vez que a proteção da espécie-chave pode contribuir direta e indiretamente à conservação das demais espécies da teia trófica, incluindo espécies raras, espécies ameaçadas, e até mesmo espécies alvo da pesca. Portanto, considerando que atualmente persistem lacunas sobre o papel ecológico dos mamíferos marinhos, nesta Tese, procurou-se desvendar quais os possíveis efeitos dos mamíferos marinhos sobre outras espécies e sobre as comunidades em diferentes ecossistemas do mundo, com ênfase na população de boto-cinza residente na Baía Norte de Santa Catarina e com o intuito maior de aplicar o conhecimento gerado nesta Tese no desenho de ações de conservação do boto-cinza e no manejo do seu ecossistema.

A MODELAGEM ECOLÓGICA COM ECOPATH WITH ECOSIM

O MODELO ECOPATH

O software Ecopath with Ecosim (EwE) foi inicialmente desenvolvido por Polovina (1984) e desde então aprimorado de maneira contínua (Christensen & Pauly 1992; Christensen et al. 2005). Ele é uma ferramenta utilizada para modelar uma rede trófica estática, ou seja, construir modelos de balanço de massa, a partir das relações de fluxo trófico entre os componentes, além de fornecer valores de indicadores ecossistêmicos e propriedades emergentes que possibilitam fazer uma estimativa da resiliência da rede trófica (Angelini 2017a,b).

Ao construir um modelo trófico, o primeiro passo é a definição de grupos funcionais (compartimentos). Os grupos funcionais devem ser definidos de uma maneira criteriosa, levando em consideração aspectos tais como: objetivos do modelo, características eco-fisiológicas similares, ora um agrupamento de espécies que possuem hábitos alimentares parâmetros vitais similares, ora por uma única espécie (normalmente espécies de valor comercial e/ou espécies-alvo de conservação). Visando refletir mudanças ontogenéticas na dieta, alguns grupos podem inclusive estar constituídos por classes etárias ou categorias de tamanho dentro de uma mesma espécie (Christensen et al. 2005). Por último, outro aspecto a considerar na definição de grupos funcionais é a disponibilidade de informações (de Araújo & de Almeida Tubino 2017).

Grupos constituídos por apenas uma espécie são considerados analiticamente vantajosos. Na equação básica de um modelo Ecopath, o consumo de um dado predador acarreta a mortalidade de suas presas por conta da predação. Após a definição dos grupos, procede-se a inclusão dos parâmetros básicos (parametrização). A inclusão dos parâmetros básicos em Ecopath é feita baseada no princípio do equilíbrio de massas. Este princípio do balanço de massas pode ser expresso conforme a equação a seguir:

$$\mathrm{Bi} \times \mathrm{PBi} = \Sigma \mathrm{Bj} \times \mathrm{QBj} \times \mathrm{DCji} + \mathrm{Yi} + \mathrm{BAi} + \mathrm{NMi} + \mathrm{Bi} \times (\mathrm{PB})\mathrm{i} \times (1 - \mathrm{EEi}) \qquad (1)$$

sendo: Bi e Bj = biomassa da presa (i) e predadores (j) respectivamente; P/Bi = produção/biomassa, normalmente equivalente a mortalidade total (Z; Allen 1971); EEi = Eficiência Ecotrófica, isto é a proporção da produção total de um grupo que é utilizada no sistema; Yi = Captura de pescado por unidade de área e tempo; Q/Ji = Consumo alimentar por unidade de biomassa de j; BAi = Biomassa cumulativa de i (positivo ou negativo); e NMi = Migração de i (emigração – imigração). A biomassa (B), a produção (PB), o consumo alimentar (QB), a eficiência ecotrófica (EE), a captura de pescado (Y) e a composição da dieta (DC) são parâmetros básicos necessários para cada grupo (i) considerado. Assim, criamos um sistema de n equações lineares, sendo n o número de compartimentos no ecossistema.

INCLUSÃO DE PARÂMETROS BÁSICOS (PARAMETRIZAÇÃO)

Ao construir um modelo de balanço de massas, o resultado é uma descrição e uma simplificação do ecossistema, refletindo os fluxos de matéria-energia, as biomassas por compartimento, além de mostrar a troca de matéria-energia entre compartimentos e a forma em que esta matéria-energia é utilizada no sistema. Logo, os dados requisitados para a construção de um modelo de balanço de massas são em geral limitados ou inexistentes, o que dificulta a construção dos modelos. É importante salientar que, para além das suas aplicações específicas (tais como manejo e conservação), estes modelos são úteis para a identificação de possíveis lacunas sobre no nosso real conhecimento do ecossistema.

Como mencionado na seção anterior, no modelo Ecopath os parâmetros básicos de entrada ("inputs") são: B (Biomassa, pode ser expressa em toneladas por km^2, t * km^{-2}), PB (Produção/Biomassa, ano^{-1}), QB (Consumo/Biomassa, ano^{-1}), EE (Eficiência Ecotrófica, valor entre 0 e 1), Captura Pesqueira (t * km^{-2} * ano^{-1}) e DC (Composição da Dieta, %). Abaixo, segue um detalhamento dos aspectos mais relevantes sobre alguns parâmetros básicos necessários para a construção de um modelo Ecopath:

PRODUÇÃO (PB): No Ecopath, a Produção é definida como toda a matéria que é elaborada por um grupo ao longo de um período de tempo determinado (no este período é anual) e considera a matéria que acaba sendo consumida por predadores, a matéria que é capturada pela pesca mais a matéria que morre por outras causas. Quando a mortalidade total é constante, ela é igual à Produção sobre a Biomassa ou taxa de Produção (P/B, ou simplesmente PB). Portanto, na construção de modelos de balanço de massa, é possível utilizar estimativas de mortalidade total (Z) como equivalentes à taxa de Produção (PB) para animais cujo crescimento de indivíduos é caracterizado pela função de crescimento de von Bertalanffy (Allen 1971). Vários métodos existem atualmente para a estimativa de Z para peixes e outros animais (Pauly 1984). Beverton & Holt (2012) corroboraram que a mortalidade total (Z = PB) em populações de peixes que crescem conforme a função de von Bertalanffy pode ser expressa da seguinte forma:

$$Z = \ PB \ = \frac{k \times (L_{\infty} - \bar{L})}{\bar{L} - L'} \qquad (2)$$

onde L∞ é o comprimento assimptótico, ou seja, o comprimento médio que alcançaria o indivíduo na população se vivesse e crescesse indefinidamente, k é a constante de von Bertalanffy (expressa a taxa de aproximação de L∞), $\bar{L}$ é o comprimento médio na população, calculado a partir de L', sendo L' o comprimento médio nas capturas. Observar que $\bar{L}$ deve ser maior que L'.

A PB é mais difícil de ser estimada para produtores primários, embora existam métodos indiretos (equações empíricas) que possibilitam a estimativa deste parâmetro para firoplâncton (Lafontain & Peters 1986), enquanto há estimativas úteis para algas bênticas e ervas marinhas (Mann 1982).

CONSUMO (QB): O Consumo por unidade de Biomassa ou taxa de Consumo (Q/B, ou simplesmente QB) é o número de vezes que uma população consome seu próprio peso por ano (Christensen et al. 2005). No Ecopath,enquanto a taxa de consumo (QB) é expresso por ano [ano-1], o consumo absoluto é expresso em termos de fluxo, por exemplo, em unidades de [t * km^2 * ano^{-1}]. Existem várias abordagens que podem ser usadas para a estimativa do QB: (*i*) métodos analíticos e (*ii*) métodos holísticos (Christensen et al. 2005). Os métodos analíticos consistem na estimativa de ingestão diária. As estimativas de ingestão diária são obtidas a partir de experimentos em laboratório, a partir de estudos de dinâmica de conteúdos estomacais na natureza (Jarre et al. 1991) ou mesmo pela combinação de estudos em laboratório e em campo (Pauly 1986). O método holístico para a estimativa de QB consiste na aplicação de regressões empíricas ou relações alométricas que possibilitam a predição de QB a partir da quantificação de características morfológicas (Palomares & Pauly 1998).

Com relação aos invertebrados, as melhores estimativas de mortalidade natural e da taxa de QB podem ser obtidas a partir dos trabalhos de Thomas Brey (1999, 2010, 2012).

Para aves marinhas, a taxa de Consumo (DR ou taxa diária de consumo de peixes em gramas) pode ser estimada a partir da equação de Nilsson & Nilsson (1976) da seguinte forma:

$$\log DR = -0{,}293 + 0{,}85 \times \log w \qquad (3)$$

onde w é o peso corporal médio da espécie (expressa em gramas). Já para mamíferos marinhos, a taxa de Consumo (DR ou taxa diária, em quilogramas) pode ser estimada a partir da equação proposta por Innes et al. (1987) da seguinte forma:

$$DR = 0{,}1\, w^{0{,}8} \qquad (4)$$

onde w é o peso médio da espécie expressa em kg.

O processo de elaboração de um modelo envolve a utilização de parâmetros derivados de fontes diversas, com diferentes graus de qualidade. As incertezas associadas com cada valor de “*input*” nos modelos Ecopath podem ser quantificadas e resumidas por meio do “Pedigree” do modelo. Para cada “*input*” que formos usar em um modelo dado, podemos dar uma “nota” que possibilite a descrição do tipo de dado e do grau de confiança que nós podemos ter naquele “*input*” em questão. Esta nota é chamada de Pedigree. Quando estas notas qualitativas são dadas para cada “input” (referentes à origem dos valores de Biomassa, PB, QB, Captura e Dieta), é possível ponderar todas e assim resumi-las em uma nota só, chamada de Pedigree global do modelo (Funtowicz & Ravetz 1990, Pauly et al. 2000). Os parâmetros necessários para a estimativa do Pedigree global do modelo normalmente podem ser dados de B, PB, QB, DC e Captura pesqueira. Os intervalos de confiança associados a cada parâmetro e atribuídos pela tabela de Pedigree podem ser definidos pelo próprio construtor do modelo ou mesmo deixados como o padrão do Ecopath.

BALANCEAMENTO E VALIDAÇÃO DE UM MODELO TRÓFICO

Em um modelo Ecopath, as entradas e saídas de todos os grupos viventes devem estar balanceadas (Christensen et al. 2005). Ao balancearmos um modelo Ecopath, assumimos que a entrada de fluxo de matéria-energia num compartimento (principalmente via consumo, embora também possa ser na forma de imigração) é igual à somatória de todas as saídas de fluxo deste mesmo compartimento (Araújo et al. 2017). Após a estimativa de parâmetros desconhecidos constituintes da produção tais como predação, captura pesqueira, migração e biomassa cumulativa para cada compartimento, podemos rodar o programa Ecopath e então proceder com o balanceamento usando a equação a seguir:

$$\text{Consumo} = \text{Produção} + \text{Respiração} + \text{alimentos não assimilados} \quad (5)$$

Quando isto não acontece, o parâmetro Eficiência Ecotrófica (EE) resulta em valores maiores que 1 (um). A EE é definida como a fração da produção total que é consumida pelos predadores e/ou capturada pela pesca. Um valor de EE maior que 1 (um) significa que provavelmente o consumo (QB) sobre este compartimento é maior do que a sua produção (PB) e/ou biomassa (B) podem suportar (de Araújo & de Almeida Tubino 2017). Portanto, podemos utilizar os valores de EE estimados por Ecopath para balancearmos um modelo (Kavanagh et al. 2004). Assim, o balanceamento consiste na identificação e modificação de valores de B, PB, QB e DC incongruentes com o princípio de balanço de massas até obtermos valores resultantes de EE que satisfaçam $0 < EE \leq 1$. Na prática, o balanceamento muitas vezes pode ser alcançado utilizando a planilha de mortalidade por predação ("Predation Mortality") do Ecopath (Christensen et al. 2005). Após a identificação do 'Máximo Predador' do compartimento mais 'desbalanceado', pode-se focar atenção sobre possíveis lacunas sobre a dieta e/ou as relações tróficas entre os compartimentos. Ou seja, a dieta daquele grupo que estiver exercendo o impacto maior sobre o grupo com o maior valor de EE, até resolver assim a equação 1. Logo após, identifica-se o seguinte grupo desbalanceado e continua-se o balanceamento até obter valores de $EE \leq 1$ para todos os grupos (Kavanagh et al. 2004).

Os modelos Ecopath são relativamente fáceis de serem construídos quando comparados com outras técnicas de modelagem e é por isso que esta abordagem tem sido amplamente utilizada (Morissette 2007). Contudo, esta vantagem acarreta dificuldades com relação à confiabilidade e qualidade dos dados utilizados para a construção do modelo (Heymans et al. 2016). Visando verificar a qualidade dos parâmetros utilizados na construção de um modelo Ecopath, algumas regras ecológicas e termodinâmicas podem ser aplicadas na hora de verificar a qualidade dos parâmetros e validar um modelo. Estas regras foram propostas por Link (2010) e são chamadas de diagnósticos PREBAL. Os critérios do PREBAL consistem em um conjunto de regras gerais ou princípios básicos que incluem: a verificação do declínio da curva de Biomassa ao longo de um gradiente crescente de nível trófico, para além do declínio de outros parâmetros vitais em função a um gradiente de nível trófico dos grupos funcionais. Assim, espera-se que quanto maior o nível trófico, menores serão os valores de

Biomassa, Produção e Consumo. Adicionalmente, é preciso considerar, como uma das regras gerais, que as estimativas de Biomassa devem abranger um intervalo de 5 – 7 ordens de magnitude (Link 2010). Referente à inclinação de parâmetros em função aos níveis tróficos dos grupos, uma das regras gerais do PREBAL estabelece que a inclinação da Biomassa (numa escala logarítmica nas ordenadas ou eixo Y) deve apresentar um decréscimo de 5 – 10 % ao longo dos grupos arranjados numa sequência crescente dos seus níveis tróficos ao longo das abscissas ou eixo X (Link 2010). Os valores de Biomassa daqueles grupos que estiverem se afastando significativamente da curva devem ser verificados. Da mesma forma que acontece com a Biomassa, os parâmetros vitais dos predadores devem ser menores que os parâmetros vitais das suas respetivas presas (Link 2010).

Um diagnóstico adicional considera a razão entre a Produção e o Consumo (P/Q), eficiência de crescimento (GE) ou razão bruta de eficiência na conversão de alimento. Este diagnóstico é baseado na segunda lei da termodinâmica e indica que um determinado grupo não pode produzir uma fração maior que aquilo que ele está consumindo (Link 2010). Como descrito por Darwall et al. (2010), a razão P/Q deve apresentar valores entre 0,1 – 0,3 para a maior parte dos grupos. A seguir, apresentam-se algumas regras ecológicas e termodinâmicas para balancear um modelo Ecopath. De acordo com Darwall et al. (2010), para um modelo Ecopath ser considerado ecológica e termodinamicamente bem balanceado, é necessário ajustar as restrições a seguir:

EE < 1,0. A Eficiência Ecotrófica (EE) é uma medida da proporção da predação que fica no sistema e que é utilizada pelos níveis tróficos superiores por meio da predação direta ou da captura pela pesca. O valor da EE (normalmente uma saída ou "output" do Ecopath) nunca pode ultrapassar 1,0, já que não é possível para um grupo repassar para os níveis tróficos superiores uma produção maior que a original, a menos que a população estivesse em declínio. A diretriz aqui é que um valor próximo de 1,0 seja o esperado para aqueles grupos cuja maior parte da sua produção é consumida pelos seus predadores ou extraída pela pesca. Um valor próximo de 0,0 é o esperado para grupos como predadores de topo uma vez que estes carecem de predadores e normalmente não são explorados pela pesca.

0,1 < GE < 0,3. A razão bruta de eficiência na conversão de alimento (GE) normalmente apresenta um valor entre 0,1 e 0,3. Valores maiores que 0,5 não são frequentes na natureza, embora possam ser encontrados para grupos como Bactérias ou em algumas espécies de peixes de criação.

Eficiência Neta > GE. Eficiência Neta é o valor da eficiência de conversão de alimento após ser descontado o alimento não assimilado (U), cujo valor padrão de Ecopath é 20 %. Certamente, o valor de GE nunca pode ser maior que a Eficiência Neta.

Respiração/ Assimilação de Biomassa (RA/AS) < 1,0. A proporção da Biomassa perdida pela respiração nunca pode ser maior que a Biomassa de alimento assimilado. Por via de regra, espera-se que espécies k – estrategistas apresentem valores próximos de 1,0, enquanto espécies r – estrategistas normalmente apresentam valores bem menores que 1,0.

Respiração/Biomassa (RA/B) indica o grau de atividade metabólica de um grupo. Espera-se a obtenção de valores entre 1 – 10 ano^{-1} para peixes, porem esses valores podem ser bem maiores, por vezes entre 50 – 100 ano^{-1} para grupos com uma alta taxa de troca de matéria, tal como costuma acontecer com grupos tais como Copépodes. O valor padrão de alimento não assimilado de Ecopath (20%) pode ser alterado para refletir melhor o valor de RA/B do grupo em questão.

Produção/Respiração (P/RA) < 1,0. Esta taxa expressa de fato o destino do alimento assimilado. Odum (1969) afirmou que P/RA, normalmente com um valor menor que 1, aproxima-se de 1 conforme o ecossistema for amadurecendo.

A orientação é que comparações entre modelos Ecopath devem ser feitas apenas quando os modelos forem verificados previamente conforme as regras do PREBAL (Heymans et al. 2016).

INDICADORES ECOSSISTÊMICOS E ATRIBUTOS COMPARTIMENTAIS

Os indicadores ecossistêmicos são normalmente usados para fornecer informações sinópticas sobre o estado de um ecossistema. A maior vantagem dos indicadores ecossistêmicos consiste que eles são capazes de combinar um conjunto de fatores ambientais e processos ecológicos em um valor só, o que facilita sua aplicação no manejo além de facilitar a compreensão de conceitos abstratos para o público geral (Marques et al. 2005, Fath et al. 2019).

O programa Ecopath também implementa uma série de indicadores ecossistêmicos desenvolvidos por ecologistas teóricos (Christensen & Pauly 1992), especialmente aqueles desenvolvidos por Ulanowicz (1986). O conjunto de indicadores e algoritmos aqui apresentado é atualmente conhecido de maneira genérica no jargão da Ecologia como Análise de Redes Tróficas (em Inglês “Network Analysis”). Nesta seção, apresentam-se brevemente alguns dos indicadores ecossistêmicos mais amplamente difundidos. A seguir apresentam-se alguns índices entrópicos de fluxo:

Total System Throughput **(TST)**: Ao trabalhar com a dinâmica trófica dos ecossistemas, tamanho e quantidade não são aferidos em termos de Biomassa, mas sim em termos de fluxo de matéria-energia (Ulanowicz 1986), sendo que fluxo é definido como a transferência de Biomassa durante certo período de tempo (a unidade de fluxo pode ser, por exemplo, $t * km^{-2} * ano^{-1}$). Assim, o TST nada mais é que a soma de todas as transferências de matéria-energia que ocorrem no sistema (Patrício et al. 2004).

Ascendência (A): A Ascendência é um conceito abstrato, porém uma propriedade emergente chave de toda teia trófica. A ascendência é derivada da teoria da informação (Ulanowicz & Norden 1990) e é definida como a informação média ponderado pelos fluxos ("System Throughput") no sistema (Christensen et al. 2005). A Ascendência pode ser definida também como uma medida que possibilita a quantificação tanto do nível de atividade quanto do grau de organização (restrição) através do qual o material é processado em sistemas autocatalíticos tais como os ecossistemas (Patrício et al. 2004, Fath et al. 2019).

Capacidade de Desenvolvimento (C): Este índice é usado para suprir a necessidade de alguma medida da complexidade da teia trófica (Monaco & Ulanowicz 1997). Em outras palavras, ele pode ser definido como a diversidade de fluxos do sistema ponderada pelo TST (Patrício et al. 2004).

Overhead **Específico do Sistema (ϕ/TST)**: A diferença entre a Capacidade de Desenvolvimento e a Ascendência é chamada de Overhead do sistema (Christensen et al. 2005). Este índice mede a flexibilidade total (resiliência) do sistema em termos de fluxos (Patrício et al. 2004). O Overhead pode ser definido como o grau em que a capacidade de sistemas abertos ultrapassa a própria Ascendência (Patrício et al. 2004) e reflete a 'reserva de forças' a partir da qual o sistema consegue se recuperar de perturbações inesperadas.

A Ascendência (A) e o *Overhead* (ϕ/TST) de um sistema específico são considerados como índices sistêmicos de informação de fluxos (Fath et al. 2019).

Eficiência Trófica: Teias tróficas que são qualitativamente muito diferentes podem ser mapeadas com um jeito simples por meio de uma cadeia trófica reta com uma topologia (isto é, número de compartimentos) padronizada, o que facilita a comparação da eficiência na passagem de energia de um nível para outro entre ecossistemas (Baird et al. 1991). A Eficiência Trófica entre dois níveis tróficos é definida como a quantidade que um nível dado passa para outro nível imediatamente superior dividido pela quantidade que o próprio nível recebeu do nível trófico inferior (Ulanowicz & Wulff 1991). A representação do fluxo de energia nas teias tróficas na sua forma canônica ou linear é chamada de Coluna de Lindemann (Ulanowicz 1997).

Índice de Reciclagem de Finn (FCI): O FCI desvenda a proporção do TST que é alocada à reciclagem de Carbono no sistema (Finn 1976). A Maturidade de um sistema dado é um conceito associado com o processo da sucessão ecológica. Odum (1969) descreveu a evolução dos ecossistemas através de um arranjo linear das relações tróficas entre seus componentes e ele também afirmava que os ecossistemas evoluem em direção para uma teia trófica complexa (em termos de troca de matéria-energia) e aumento no uso de matéria procedente dos detritos, ao invés de basearem o seu sustento só nos produtores primários, o que acontece em sistemas menos desenvolvidos. É por causa disto que a relação entre a somatória dos fluxos baseados nos detritos sobre a somatória dos fluxos baseados nos organismos autotróficos, ou também chamada razão de herbivoria já foi usada em trabalhos pretéritos para ponderar o grau de maturidade dos ecossistemas (Christensen 2005). A maturidade é correlacionada forte e negativamente com a Ascendência relativa, logo ela apresenta uma correlação forte e positiva com o *Overhead* do sistema; este último por sua vez é uma medida de estabilidade além de ele ser considerado uma medida mais adequada de Maturidade (Christensen 1995). Com relação à reciclagem de matéria no ecossistema, Odum (1969) afirmou que quanto maior for a Maturidade do sistema, maior a porcentagem de matéria e energia reciclados, logo maior o FCI. Contudo, mais do que refletir Maturidade, a reciclagem parece ser uma medida de Estresse (Baird et al. 1991).

Índices de Espécie-Chave: Uma espécie-chave é definida como uma espécie com uma abundância/biomassa relativamente baixa que cumpre um papel preponderante na estruturação da teia trófica (Libralato et al. 2006, Heithaus et al. 2008). A identificação de espécies-chaves em um contexto ecossistêmico pode ser uma tarefa importante na hora de nos engajarmos em prol da Conservação ou até mesmo visando a sua aplicação no Manejo de ecossistemas (Fath et al. 2019), visto o potencial de algumas espécies de poderem desencadear cascatas tróficas. A seguir, há uma revisão e descrição da análise da Matriz Integral de Impacto Trófico ("MTI", pelas siglas do Inglês "Mixed Trophic Impact") e dos índices de espécie-chave ("KS", pelas siglas do Inglês "Keystone Species" ou "Keystoneness").

Conforme o modelo Ecopath foi sendo desenvolvido, diversos módulos foram acrescentados ao programa, tal como aconteceu com o módulo de *Network Analysis*, atualmente disponibilizado com o modelo Ecopath (Christensen et al. 2008). *Network*

Analysis compreende especialmente a Matriz Integral de Impacto Trófico (*M*) mais a análise de espécie-chave. A *MTI* foi trazida à Ecologia como uma adaptação ao estudo de teias tróficas a partir da análise econômica de entradas-saídas (Ulamowicz & Puccia 1990) e posteriormente implementada em Ecopath (Christensen & Walters 2004). A MTI é calculada a partir de uma matriz n x n, cujos elementos (m_{ij}) representam o impacto relativo do grupo impactante *i* sobre o grupo impactado *j* para cada par de grupos (i, j) na teia trófica modelada, considerando as interações tróficas diretas (predação) e indiretas (competição) (Ulanowicz & Puccia 1990, Christensen & Walters 2004). O m_{ij} também é estimado para cada frota pesqueira definida no modelo, sendo que estas são consideradas como predadores no sistema (Christensen & Walters 2004). A matriz de impacto trófico, M, é obtida a partir da matriz n-dimensional de impactos netos, *Q*, sendo que os elementos q_{ij} são calculados como a diferença entre os efeitos positivos quantificados a partir do termo de composição da dieta (DC_{ji}), e os efeitos negativos expressos pelo termo de composição do hospedeiro (FC_{ij}):

$$q_{ij} = DC_{ji} + FC_{ij} \tag{6}$$

onde DC_{ji} é a proporção do grupo *i* na dieta do grupo *j*, e FC_{ij} é a proporção do grupo *j* no consumo do grupo *i* (Ulanowicz & Puccia 1990, Christensen & Walters 2004). Para grupos não viventes, DC_{ji} é assertado como zero, enquanto para as frotas pesqueiras DC_{ij} representa a proporção do grupo *i* na captura da frota *j* (Christensen et al. 2008). O impacto trófico m_{ij} é então obtido como o produto de todos os impactos líquidos s q_{ij} para todas as possíveis passagens na teia trófica que ligam os grupos funcionais *i* e *j* (Ulanowicz & Puccia 1990, Libralato et al. 2006, Valls et al. 2015) da seguinte forma:

$$[M] = \{[I] - [Q]\}^{-1} - [I] \tag{7}$$

Assim, as equações 6 e 7 possibilitam o cálculo da matriz de impacto trófico (*MTI*).

Dois índices usados para medir o quanto uma espécie possui o potencial para ser considerada uma espécie-chave (“keystoneness” ou simplesmente *KS*) foram implementados inicialmente, enquanto *KS* análise, dentro do módulo Network Analysis no EwE (Christensen et al. 2008). O primeiro índice, chamado *KS1* no EwE foi proposto por Libralato et al. (2006), já o segundo, chamado *KS2* no EwE, foi uma adaptação da metodologia proposta por Power et al. (1996). Ambos os índices são estimados baseados nos mesmos parâmetros: uma medida do impacto trófico (TI_i), derivada da análise de *MTI*, e uma medida da biomassa (p_i). O parâmetro TI_i representa o efeito global do grupo *i* sobre todos os demais grupos da teia trófica (excluindo o efeito do grupo sobre si mesmo)

$$TI_i = \sqrt{\sum_{j \neq i} m_{ij}{}^2} \qquad (8)$$

onde TI_i é expresso como a somatória dos quadrados dos valores de m_{ij} do grupo *i* pareado com cada um dos demais grupos vivos *j* na teia trófica. São excluídos tanto o impacto trófico integral de *i* sobre si mesmo como o impacto sobre grupos mortos como detritos (Libralato et al. 2006).

O parâmetro p_i corresponde à contribuição do grupo *i* para a biomassa total na teia trófica

$$p_i = \frac{B_i}{\sum_{k=1}^{n} B_k} \qquad (9)$$

onde B_i é a biomassa do grupo *i*, e B_k a biomassa de cada um dos *n* grupos vivos da teia trófica (Power et al. 1996, Libralato et al. 2006).

Os índices *KS1* e *KS2* são obtidos pela combinação dos parâmetros TI_i e p_i para cada grupo (Power et al. 1996, Libralato et al. 2006) da seguinte maneira

$$KS1 = log[TI_i \times (1 - \mathrm{p_i})] \qquad (10)$$

$$KS2 = log[TI_i \times (1 / \mathrm{p_i})] \qquad (11)$$

Em ambos os índices, *KS1* e *KS2*, *KS* é estimado baseado em dois componentes: (1) um componente estimando o impacto trófico de um grupo (IC), e (2) um componente estimando a biomassa do grupo (BC) (Valls et al. 2015). Assim, uma equação geral para um índice *KS* pode ser expressa genericamente da seguinte forma:

$$\mathrm{KS}i = log[\mathrm{IC}i \times \mathrm{BC}i]. \tag{12}$$

Posteriormente, após o trabalho de Valls et al. (2015), mais um índice KS, chamado KS3 no EwE, foi incorporado ao módulo *Network Analysis* do EwE. Em KS3, BC não é calculado a partir de uma proporção, mas sim a partir da colocação do grupo conforme sua contribuição de biomassa ("ranking") em uma ordem decrescente (Valls et al. 2015). Os resultados de Valls e colaboradores indicam que KS3 é o índice mais balanceado em termos de contribuição dos dois componentes (IC_i e BC_i) para o valor de KS.

Embora estes índices são indicadores determinísticos, várias evidências corroboram a existência de espécies-chaves em diversos ecossistemas, tanto marinhos como terrestres. Como alguns exemplos paradigmáticos, podemos mencionar o caso dos efeitos documentados após a exclusão (em 1920) e posterior reintrodução (em 1995) do lobo no Parque Nacional do Yellowstone nos Estados Unidos (Berger et al. 2008) ou mesmo o caso da virtual exclusão da lontra na costa Oeste da América do Norte a partir de 1741 até a sua posterior recuperação após medidas de proteção terem sido implementadas a partir de 1911 (Estes & Palmisano 1974). Embora algumas espécies-chaves possam apresentar relativamente poucas interligações (conexões) com outros componentes (em termos de troca de matéria-energia), espécies-chaves se caracterizam por influenciar fortemente o ecossistema como um todo, como o que acontece com o paradigmático caso da estrela de mar *Pisaster ochraceus* descrito por Paine (1969), que é considerado como um exemplo clássico de espécie-chave amplamente mencionado na literatura da Ecologia até a atualidade.

PREMISSAS, HIPÓTESES E OBJETIVOS

A partir da contextualização exposta acima, a presente Tese levanta a seguinte pergunta inicial: existe algum tipo de padrão em larga escala global no papel ecológico dos principais grupos de mamíferos marinhos? Quais são os fatores subjacentes que podem afetar o papel ecológico dos mamíferos marinhos? Em uma escala fina, regional, soma-se à pergunta inicial: qual o papel ecológico do boto-cinza (*Sotalia guianensis*) na Baía Norte de Santa Catarina? É possível deduzir qual o grau de vulnerabilidade da população mais austral da espécie?

Visto que (*i*) os mamíferos marinhos habitam uma vasta gama de ecossistemas aquáticos em praticamente todos os grandes corpos d'água ao redor do mundo; (*ii*) que eles podem variar significativamente no nível trófico em que eles se alimentam; (*iii*) que apresentam grande variação tanto na abundância/biomassa como nos seus respectivos portes - e parâmetros vitais associados; (*vi*) que há variações latitudinais na produtividade primária nos mares do mundo, sendo que isto pode estar associado à disponibilidade de recursos alimentares utilizada pelos mamíferos marinhos; (*v*) que quanto maior o nível trófico, maior a probabilidade de ocorrerem cascatas tróficas e interações indiretas; e (*vi*) visto que tanto a biomassa como os parâmetros vitais são características que podem estar associadas ao papel ecológico dos mamíferos marinhos; esta Tese levanta as seguintes hipóteses:

- Existe variação e padrão no papel ecológico dos principais grupos de mamíferos marinhos em diferentes ecossistemas ao redor do mundo;

- A posição na rede trófica, aferida em termos de nível trófico, é um fator importante para a definição do papel ecológico dos mamíferos marinhos;

- A biomassa e parâmetros vitais tais como e a taxa de consumo, afetam o papel ecológico dos mamíferos marinhos, uma vez que estes parâmetros variam significativamente entre espécies e entre populações em diferentes ecossistemas;

- O boto-cinza (enquanto compartimento) residente na Baía Norte de Santa Catarina apresenta uma função ecológica crucial, sendo uma espécie-chave dentro do ecossistema;

- A população do boto-cinza da Baía Norte de Santa Catarina é vulnerável a eventuais mudanças no ecossistema, tais como a remoção de outros componentes do ecossistema; e

- Existem compartimentos (componentes) centrais na teia trófica da Baía Norte de Santa Catarina, sendo que tais compartimentos podem estar ligados diretamente com o boto-cinza.

Objetivo geral

Realizar um estudo sistemático sobre o papel ecológico dos mamíferos marinhos, com ênfase na população residente de Boto-cinza na Baía Norte de Santa Catarina.

Objetivos específicos

- Conduzir uma série de meta-análises de “outputs” e meta-dados modelos Ecopath construídos ao redor do mundo com o intuito de explorar possíveis padrões no papel ecológico dos mamíferos marinhos e desvendar possíveis fatores que possam estar afetando a função ecológica dos principais grupos de mamíferos marinhos (Capítulo 1).

- Construir um modelo Ecopath da teia trófica da Baía Norte de Santa Catarina objetivando desvendar o papel ecológico do boto-cinza, sua possível vulnerabilidade, além de aplicar ferramentas de análises de redes tróficas objetivando possibilitar a identificação de compartimentos centrais no ecossistema (Capítulo 2).

CAPÍTULO 1: The role of mammals as key predators in marine ecosystems

ABSTRACT: Marine mammals are believed to exert a strong influence on ecosystems, though the best methods for measuring their ecological role have long been discussed. Here, we use an ecosystem modeling approach to explore the underlying forces that define their ecological role, with a focus on predatory effects. We used the outputs and metadata from 55 food web models built using Ecopath with Ecosim software to analyse the effects of several likely explanatory variables on two indices of trophic significance: the relative total impact (TI) and the "keystoneness" index (KS). Our results show that both the TI and KS are positively related to trophic level. We also found an additional effect of group biomass in both TI and KS, but this response was clade-dependent: the higher the biomass, the higher the TI and KS of odontocetes and pinnipeds, suggesting that food intake contributes to the ecological role of these clades. We did not detect a latitudinal pattern in the ecological role of any clades. We also found no effects of metabolic rates on TI and KS. In sum, these findings suggest that: (i) the ecological role of marine mammals is mainly defined by their trophic levels and food intake, via biomass variation; and (ii), since odontocetes and pinnipeds feed on higher trophic levels and have higher trophic impact, these two clades can be more vulnerable to competition from fisheries overexploitation. Our meta-analytic approach contributes to the understanding of predatory effects of marine mammals on different ecosystems.

Keywords: Marine mammal · Ecopath · Trophic impact · Keystoneness · Trophic level · Consumption .

INTRODUCTION

The ecological role of organisms—their effects on associated species, communities, and ecosystems—can be evaluated in many ways. We can describe how a species is linked to the interactive food web (Menge & Sutherland 1987), for example, and then characterise the dynamic nature of those relations by manipulating systems, perturbing their drivers, and then measuring their responses (Estes et al. 2016). These manipulations, however, are logistically challenging (Englund & Cooper 2003), and other approaches must be considered. One alternative is ecosystem modelling, with approaches that can be particularly useful when manipulations are not feasible and data is missing. Specifically, food web models utilise predation processes as the primary drivers shaping both the ecological roles of trophic groups and ecosystem functioning in terrestrial and marine environments (Glen & Dickman 2005). The ecological importance of marine mammals is typically based on examinations of their trophic ecology; however, only a few case studies have presented reliable examples regarding their precise ecological roles (Baum & Worm 2009, Estes et al. 2016, Carlucci et al. 2020). Since investigations on the role of marine mammals in their environments are quite challenging (Bowen 1997), quantitative assessments of the predatory effects of marine mammals and the comparison of such effects across different ecosystems types are needed (Estes et al. 2016). Current investigations on the impacts of species loss or population decline should be expanded beyond experimental research to include multilevel food webs (Duffy 2002). Steady-state, mass-balanced food web models can be used to explore the role of marine mammals through two approaches: assessment of the interaction strength using diet composition information and quantification of food intake.

Marine mammals thrive on a variety of food resources, and the variation in the trophic level (TL) of their prey is critical to understanding their ecological role. Among cetaceans, mysticetes feed mainly on planktonic crustaceans and small fishes in dense aggregations, using ram and lunge filtration (Pivorunas 1979). Small odontocetes feed mainly on large demersal and pelagic fishes and schooling squids. The deep-diving sperm whales (*Physeter macrocephalus*), pygmy sperm-whales (Kogia spp.), Ziphiidae Family, and Globicephala spp. mainly feed on large and solitary squids. *Orcinus orca* and *Pseudorca crassidens* are top predators that prey on other top predators such as pinnipeds, marine birds, sharks, salmon, and other cetaceans (see Ballance 2009 for a review). Pinnipeds typically feed on a range of organisms similar to those observed for small odontocetes (Pauly et al. 1998). Many of these predators are more vulnerable to extinction, which in turn can weaken top-down control pathways (Duffy 2002, Notarbartolo di Sciara 2002, Heithaus et al. 2008). Thus, knowledge about diets can help us assess the predatory effects and likely vulnerabilities of marine mammals.

The mixed trophic impact matrix (Ulanowicz & Puccia 1990), as derived by Hannon (1973) from the Leontief (1951) input-output network analysis, uses diet information as a key tool for ecological role assessments. Network analysis considers both the direct and indirect effects of changes in the biomass of each species upon other species; it considers all pathways of all lengths in a food web; it expresses the relative biomass changes for all compartments resulting from an infinitesimal biomass gain in the compartment being assessed (Ulanowicz & Puccia 1990). This trophic impact attribute can be used to assess the feed interaction strength of the species on the other compartments in the ecosystem.

The trophic interaction strength measure and the relative biomass of the species can be combined to evaluate the ecological role in terms of its keystoneness, which is defined as a species showing a disproportionate effect on the community despite its relative low abundance/biomass (Libralato et al. 2006). In fact, keystone species have a substantial effect on other species and food web resilience (Libralato et al. 2006, Jordan 2009). Keystone species drive ecosystem dynamics through processes such as habitat modification, hosting other species, and predation, by controlling the density of competitor and prey species (Mills et al. 1993, Piraino et al. 2002). A keystone species has a greater impact on biodiversity and trophic structure than other species with similar or higher abundance in the ecosystem (Paine 1969). It is generally defined as relatively low biomass species that plays a structural role in food webs (Libralato et al. 2006, Heithaus et al. 2008) and the removal of such keystone species can cause huge changes in their communities (Power et al. 1996).

Another approach to assess the ecological role of marine mammals involves energy flows to quantify food intake. Food intake is the product of the biomass of a living group (*B*) multiplied by its consumption/biomass ratio (*QB*) expressed as a ratio (t·km-2·year-1) (Christensen et al. 2008). Food consumption was previously used to highlight the ecological role of marine mammals (Katona & Whitehead 1988, Spitz et al. 2018). They can exert a major influence on the structure and functioning of ecosystems due to their the amount of prey consumption, which is related to their large body sizes, abundance, or relatively high metabolic rates (Estes 1979, Bowen 1997). Indeed, some alternative indices, such as the surface index (SI, which is associated with specific metabolic rates) have been used to measure the ecosystem impact of marine mammals on food webs (Morissette & Brodie 2014). These indices show that the species energetic requirements per unit of biomass may diminish with body size (West et al. 1997). Interestingly, it seems that the mixed trophic impacts derived from the network analysis might correlate to SI impacts for some species of marine mammals (Morissette & Brodie 2014).

Marine mammals also may play other numerous roles in marine ocean ecosystems other than predators, including as prey, detritus, and vectors of nutrients (Roman et al. 2014, Roman & Estes 2017). The ecological role of species in marine communities, however, typically focuses on trophic relationships. Predation is the most ubiquitous and essential of species interactions (Estes 2009). Otherwise, the effect of biomass on food intake of mammals in marine ecosystems can vary because of different adaptations, distribution of food, and the effect of human activities in reducing marine mammal populations (Forcada 2009). In addition, marine mammal distribution strongly correlates to net primary production and net secondary production, and these production rates vary with ecological conditions across the globe (Huston & Wolverton 2011). Thus, the following question remains: is there a general pattern in the predatory effects of the major marine mammal groups along a latitudinal gradient, even among different ecosystem types around the world?

Investigations of marine ecosystems, including the role of top predators, typically involve complex sampling processes, and the associated costs are generally high (Bowen 1997, Morissette 2007). food web models can be a useful tool to separate, simplify, and understand the multiple drivers, structure, and mechanisms behind the functioning of marine ecosystems and their components. Mass-balance (i.e. steady-state) food web models, for example, can help us explore how species influence each other (Blanchard et al. 2002, Hernandez-Milian et al. 2015). These trophic models can provide a means to probe the predatory effects of functional groups (species or groups of species) in different aquatic ecosystems (Coll et al. 2013, Pan et al. 2016, Bornatowski et al. 2017), helping us to overcome the typical constraints associated with marine ecosystem investigations.

Among the several modelling approaches developed in recent decades, the Ecopath framework (Polovina 1984) is likely to be the most suitable to explore the ecological role of mammals in aquatic ecosystems (Morissette 2007). Ecopath has proven advantageous in modelling numerous ecosystems worldwide. For example, Ecopath allows the estimation of missing parameters of some compartments and the quantification of trophic relations among the most important functional groups in an ecosystem. Ecopath also has a platform, EcoBase (Colléter et al. 2013, Colléter et al. 2015), that provides access to other data sets enabling researchers to make comparisons and search for patterns across multiple systems, which is an important goal for marine science (Estes et al. 2016). To date, only few studies have been conducted taking a meta-analytical approach by using a set of model collections to investigate marine ecosystems (e.g., Coll et al. 2013, Heymans et al. 2014). Nevertheless, these collections are not open access, which prompted the creation of the EcoBase repository (Colléter et al. 2015).

Here, we use a meta-analytic approach to assess the ecological role of marine mammals across different marine ecosystems and latitudes. We synthesise available information from several published Ecopath food web models available in EcoBase that included marine mammal groups to assess their trophic position, ecological role, and food intake. We test if trophic position of marine mammals (in terms of trophic levels) affects their interaction strength and their importance as keystone species. We also test if keystoneness and trophic impact are mediated by metabolic rates and food intake—in terms of consumption/biomass (QB), body size, and group biomass. Finally, we discuss how our meta-analytic approach can be valuable to overcome the methodological constraints impeding the assessment of the ecological role of mammals in marine ecosystems and the implications of our results for marine ecosystem-based management.

MATERIALS & METHODS

ECOPATH MODELS

Ecopath is a modelling framework based on the ecosystem approach originally proposed by Polovina (1984). Since its creation, Ecopath has been under continual development (Christensen & Pauly 1992, Christensen & Walters 2004, Christensen et al. 2008). Parameterization for Ecopath models is based on the steady-state principle, which assumes all functional groups/species are mass balanced. Ecosystem models can be constructed with Ecopath based on interspecific feeding relationships in a trophic network. The simplest mass-balance Ecopath master equation for each functional group (i) can be expressed as:

$$Bi \times PBi = \Sigma Bj \times QBj \times DCji + Yi + BAi + NMi + Bi \times (PB)i \times (1 - EEi) \qquad (1)$$

where: Bi is biomass of prey i, PB_i is the production-biomass ratio (PB) of i, B_j is the biomass value of predator j, QB_j is the consumption-biomass ratio of predator j, DC_{ji} is the diet composition or proportion of prey i in the diet of predator j, Y_i is the total fishery catch of i, BA is the biomass accumulation rate for i, NM is the net migration rate (emigration—immigration) of i, EE is the ecotrophic efficiency, and ($1-EE_i$) is mortality other than predation and fishing. An Ecopath mass-balance model provides a 'snapshot' quantified by the flows throughout the food web. Ecopath is able to compute many ecosystem and ecological attributes, including, in our case, the trophic impact of a group on other species and a set of keystoneness indices (Christensen & Pauly 1992, see also http://www.ecopath.org).

Here, we used the input-output data and metadata from 55 Ecopath models constructed worldwide (details in Supplementary Material — Table S1). We used EcoBase, which is an online repository featuring information from more than 400 published Ecopath with Ecosim (EwE) models (Colléter et al. 2013) to extract basic parameters and ecosystem attributes of marine mammal functional groups. We assumed that the 55 Ecopath models analysed here were constructed independently, especially the parameter values of marine mammals, so we assumed food web constructors used local samplings and references.

In a food web, the prey of a certain predator may have different trophic positions. The trophic position of species can be quantified and expressed in terms of their trophic level (*TL*; FAO 2020). The *TL* of a predator *j* can be defined using the *TL* of all its prey as follows:

$$TL_j = 1 + \sum_i^n C_{ji} * TL_i \qquad (2)$$

which means that the *TL* of a predator j is defined by the *TL* of all its prey (i = 1, 2, ..., n) weighted by the proportion of the prey i in the diet of predator j (C_{ij}), n being the total number of food prey types in the food web. Customarily, the *TL* of primary producers and detritus are equal to 1.

COMPARTMENTAL ATTRIBUTES

To explore the ecological role of marine mammal species within food webs, we used two main ecological attributes as response variables: the relative total impact (*TI*) and a keystoneness index (*KS3*). *TI* is defined as the percentage of a compartment's activity that could affect and is being affected by, either positively or negatively, any other compartment (both in direct and indirect ways through the food web). TI values range between 0 and 1, with values close to 1 indicating higher trophic impact. This index is based on the mixed-trophic impact (*MTI*) matrix, which can be used to quantify the effect that changes on a species/trophic group biomass would have on the biomass of other groups (Ulanowicz & Puccia 1990). Then, the net impact of i on j (q_{ij}) is given by the difference between positive effects, quantified by the fraction of the prey i in the diet of the predator j (d_{ji}), and negative effects, evaluated through the fraction of total consumption of i used by predator j (f_{ij}). Therefore, the resulting matrix of the net impacts (Q) will have the following elements:

$$q_{ij} = d_{ji} - f_{ij} \tag{3}$$

The mixed trophic impact (m_{ij}) is then estimated by the product of all the net impacts (q_{ij}) for all the possible pathways in the trophic web that link the functional groups i and j. *TI* is then computed, excluding the mixed trophic impact of the consumer on itself, as well as on dead groups such as detritus (Libralato et al. 2006) from m_{ji}, as follows:

$$TI_j = \sqrt{\sum_{j \neq i}^{n} m_{ji}^2} \tag{4}$$

The other attribute used in this study is the keystone species index (*KS*), which is estimated based on two components: *i*) the trophic impact (*TI*) of the group (also referred to as the impact component), and *ii*) the biomass component (Libralato et al. 2006). Ecopath estimates three types of KS indices (*KS1*, *KS2*, and *KS3*). These three indices differ in the way the biomass component is computed among equations. Whereas the biomass component of KS1 and KS2 is computed based on an algorithm that weighs the proportion of the biomass of the functional group observed in the ecosystem, the biomass component of KS3 is estimated based on the rank of the biomass variable, with a ranking in descending order (Valls et al. 2015). The *KS3* index is calculated as shown below:

$$KS3 = IC \times BC \tag{5}$$

where IC is the impact component (IC = TIj) and BC is the biomass component (BC = drank (Bi), while drank designates the rank of the biomass component. Here, we used the KS3 index, which is the newest index, as it seems to have the best balance between the impact and biomass components (Valls et al. 2015). We then took the KS3 ranking position of marine mammals among all components of each Ecopath model as our keystoneness response variable (KS). We highlight that, although the TI and the KS indices are not independent, they give insights about different aspects of the ecological role (TI for interaction strength and KS for keystoneness). Furthermore, while the TI is an adjusted index (i.e., it ranges between 0 and 1, with values close to 1 indicating higher trophic impact), the KS3 is not, which means that KS3 scores cannot be compared across ecosystem models. This is why we assessed the relative KS3 ranking positions rather than on the KS3 scores. We obtained our KS ranking position by dividing the KS3 scores sorted in ascending order by the total number of groups (excluding detritus groups) in the model. Our new keystoneness index (KS) also ranges between 0 and 1.

DATA ANALYSIS

We first applied graphical tools to explore and test correlations between all explanatory and response variables used in our study (Zuur et al. 2010). During this data exploration, we also modelled consumption/biomass ratio (*QB*) as a function of body size, and trophic level (*TL*) as a function of clades. These previous analyzes guided us to build the linear models that investigated how the trophic impact (*TI*) and the keystoneness index vary.

We then used a beta generalized linear mixed model (GLMM), with a logit link function (Zuur et al. 2010) to investigate the trophic impact (*TI*) of marine mammal functional groups as a function of trophic level (*TL*), consumption/biomass ratio (*QB*), the biomass of the marine mammal group in the ecosystem and latitude of the ecosystem, adding clade, mysticetes, odontocetes, or pinnipeds, as an interaction term in each covariate. Ursoidae (polar bears) and Lutrinae (otters) occurred only in one model each, and therefore they were not considered in our analysis. We then modelled the keystoneness index response variable as a function of *TL*, *QB*, the biomass and the latitude, adding clade as an interaction term in each covariate, also using a beta GLMM with a logit link function (Zuur et al. 2009). We note that *TL*, *QB*, and the group biomass are directly or indirectly included in the *TI* and *KS* equations, so they are likely correlated. We included these variables to explore how each one contributes to the *TI* and *KS* values. For both sets of models, we added the ecosystem type—defined as open ocean, Arctic shelf, temperate coastal and shelf areas, and tropical coastal and shelf areas—as a random factor, to account for variations in ecological conditions. By adding *TL* as a covariate in these models, we investigated the effect of the trophic position in the ecological roles of marine mammals (i.e., the trophic impact and keystoneness). By adding *QB* as a covariate, we investigated the effect of metabolic rates in the predatory effects. Our data exploration showed that indeed *QB* diminishes with body size (see Consumption/biomass ratio (*QB*) as a function of body size, Figure S1 and Table S1 at Supplementary Material—SM2). By adding the total biomass of the marine mammal group in an ecosystem as a covariate, we investigated how sensitive our ecological role indices were to variations in food intake. We added the latitude of each ecosystem as a covariate because marine mammal distribution and abundance depends on ecosystem production rates, which can vary latitudinally. Finally, we added clade as a covariate or interaction term combined with the other covariates, because our data exploration suggested that the relationship between our explanatory variables and the trophic impact and keystoneness behaves differently across clades (see Figure 1 at results section for further detail).

All models were considered additive or interactive (for clade) relationships between the explanatory variables. All models and graphs were performed in R (R Core Team 2019). Models were fitted using the 'glmmTMB' package (Magnusson et al. 2017). Model variables were selected by stepwise backward elimination from full models, using Akaike's information criterion (AIC) and Akaike weights to rank and find the most parsimonious model by favouring the model with the lowest AIC. We considered fitted models to be those with ΔAIC (model-minimum) < 2 (Burnham & Anderson 2002). For AIC and Akaike weight calculation, we used the R package 'MuMIn' (Barton & Barton 2015). Scaled residual checking was executed with the DHARMa package (Hartig 2018; see Models validation Supplementary Material—SM2). The significance level in all statistical tests was 95% ($p < 0.05$).

RESULTS

The input-output data and metadata from 157 marine mammal functional groups from the 55 Ecopath models considered in this study are presented in the SM1. The total average number of functional groups in the 55 trophic models is 31.73 ± 11.43 (SM1). These models presented five marine mammal clades: odontocetes (40 models), mysticetes (23 models), pinnipeds (24 models), Ursoidae, and Lutrinae (one model each). Polar bears and sea otters could not be included in these analyses because of the low number of replications.

Our first results from our exploratory analyzes showed there is a significant differentiation on the trophic levels of the three main taxonomic groups assessed in our study (see Trophic levels by Clades and Figure S2 at SM2). mysticetes feed on a lower trophic level when compared with the other two clades (odontocetes Estimate = 0.173; z = 0.019; $p < 0.01$; Pinnipedia Estimate = 0.098; z = 0.023; $p < 0.01$; see Trophic level by clades at SM2). From our correlation exploratory tests, we found a clear relationship for all clades between *TI* and *KS* (r = 0.85; $p < 0.05$; Figure 1), as we expected. Then, we found that trophic level (*TL*) and consumption/biomass ratio (*QB*) seem to correlate with both *TI* and *KS* only for mysticetes (*TL*: r = 0.60; $p < 0.05$; *QB*: r = 0.53; $p < 0.05$; Figure 1). As also expected, we found a slight correlation between Mysticete biomass and latitude (r = 0.41; $p < 0.05$; Figure 1).

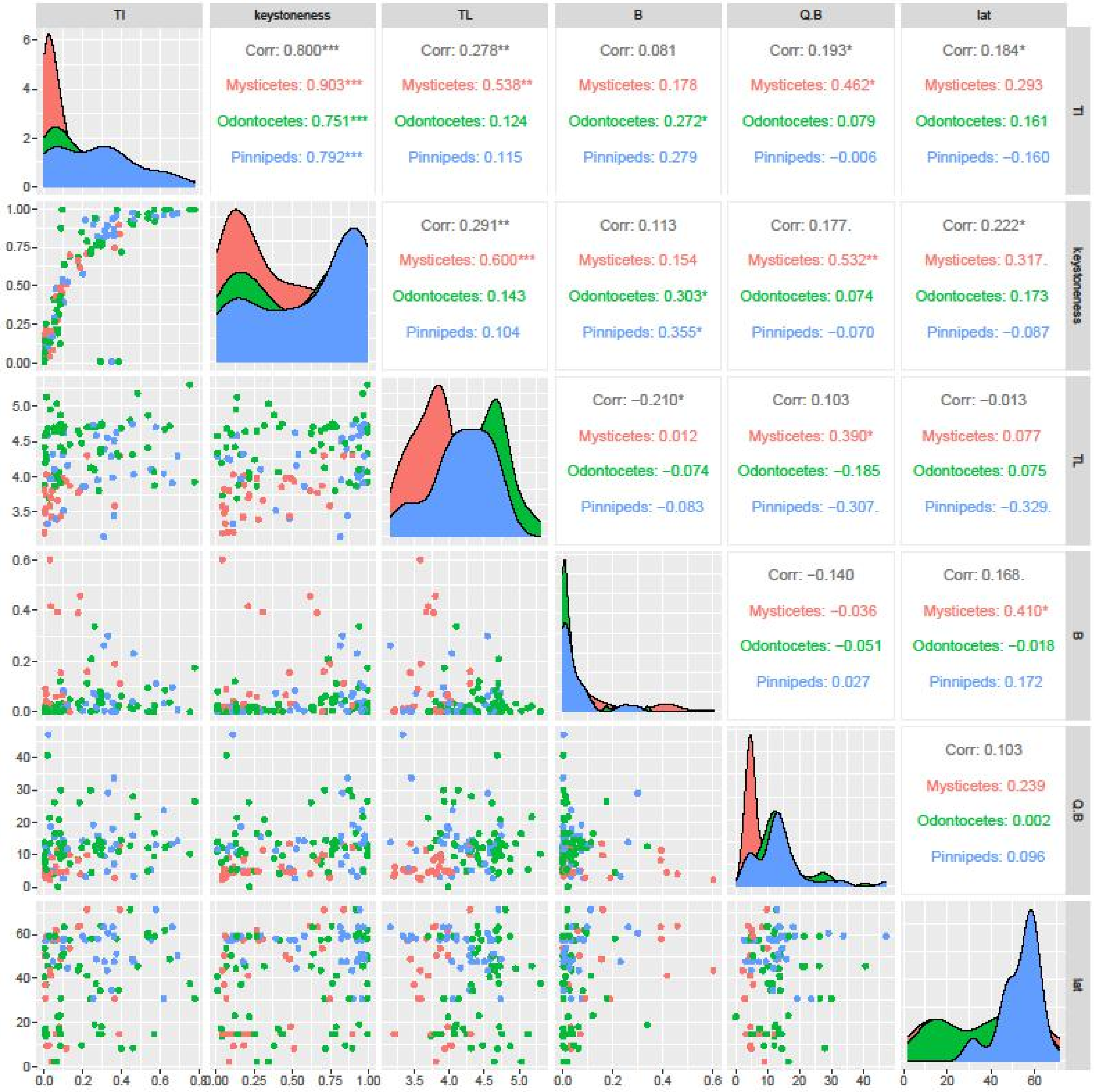

Fig. 1. Pair plot for the correlations between all variables. Lower triangle shows row data; diagonal shows density distributions; upper triangle shows person correlation results. Results are separated by clades: Mysticetes (red), Odontocetes (green), Pinnipeds (blue). *shows statistically significant.

Table 1. Model selection for the two sets of generalized mixed models for Trophic Impact (TI) and keystoneness index (KS) with Trophic Level (TL), consumption-biomass ratio (QB), the biomass (B) of the marine mammal functional groups and the ecosystem latitude (lat) as explanatory variables. All variable values are from 55 Ecopath models (see text). Models are ranked by the adjusted Akaike information criterion (AICc). * indicates an interaction term; ‘df’ = degrees of freedom, ΔAICc = difference between the AICc of the model and the minimum AICc; ‘wi’ = AIC weights; ^{nv} indicates models that did not validate

Rank	Models	df	logLik	AICc	ΔAICc	w_i
1	**TI~TL+B*clade**	**9**	**90.13**	**-160.6**	**0**	**0.444**
2	TI~TL+B+clade	7	87.20	-159.4	1.22	0.241
3	TI~TL+QB+B+clade	8	87.90	-158.5	2.12	0.154
4	TI~TL*clade +B	9	88.56	-157.5	3.14	0.092
5	TI~TL+QB+B+clade+lat	9	88.26	-156.9	3.73	0.069
1^{nv}	KS~TL+B+clade+lat	8	26.71	-36.2	0.00	0.289
2^{nv}	KS~TL+B+clade	7	25.48	-36.0	0.18	0.265
3	**KS~TL+B*clade**	**9**	**27.70**	**-35.9**	**0.33**	**0.245**
4	KS~TL+QB+B+clade+lat	9	27.06	-34.6	1.61	0.129
5	KS~TL*clade +B	9	26.49	-33.4	2.82	0.071

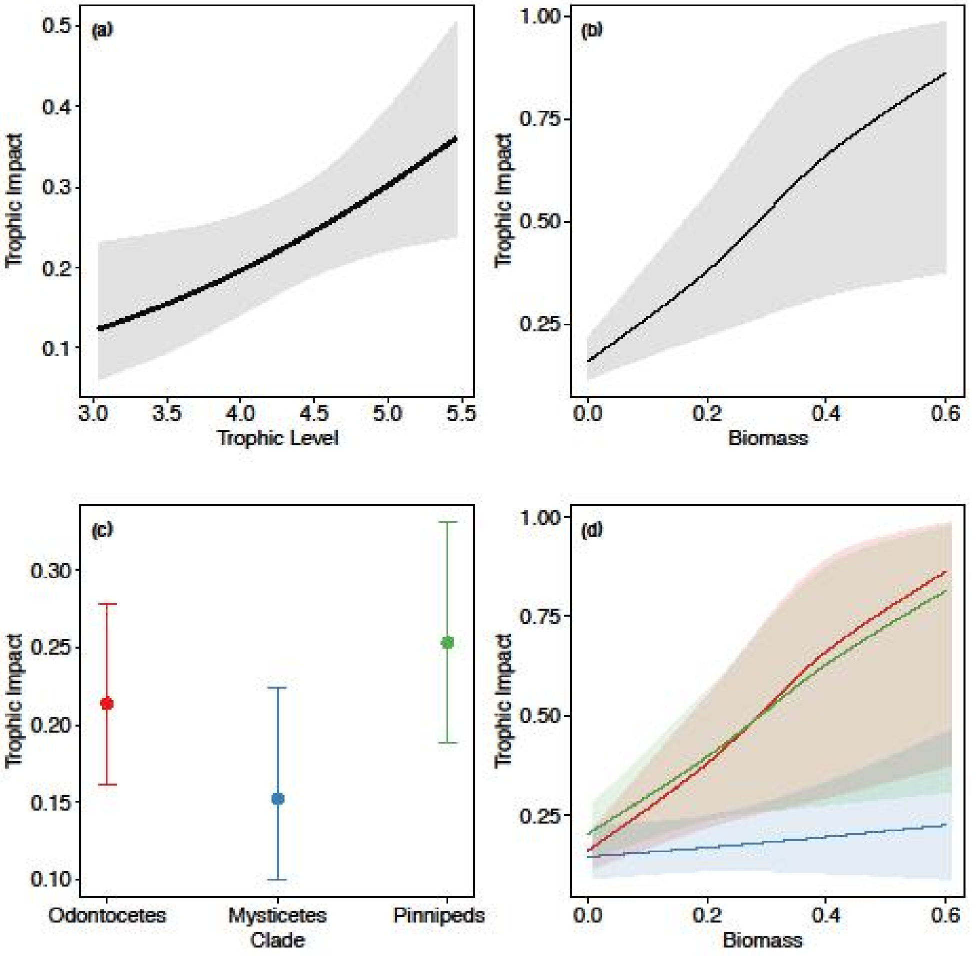

Fig. 2. **Trophic impact as a function of trophic level, group biomass, clade, and biomass per clade**. Predicted effect of *TL* on Trophic Impact (*TI*) (a); Predicted effect of group biomass on *TI* (b); Predicted effect of clades on *TI* (c); Predicted effect of group biomass by clades on *TI* (red lines = odontocetes; blue lines = mysticetes; green lines = pinnipeds) (d). Shaded areas represent the 95% confidence interval of predicted values. All variables were taken from 157 marine mammal functional groups in 55 Ecopath models (see section 2.1). Points are predicted values. Bars represent the 95% confidence interval of predicted values.

The most parsimonious (validated) model from our second set of models showed that there is a significant effect of *TL* on the keystoneness index (*KS*) of the 157 marine mammal functional groups in the 55 Ecopath models (Table 1; Model 3: *TL* estimate = 0.571; z = 2.102; p = 0.03; Figure 3a). This model also showed that the biomass of the marine functional group affects *KS*, and this effect is clade dependent, having been more noticeable for odontocetes (Model 3: Biomass estimate = 6.145; z = 3.175; p = 0.05; marginal effect) than for mysticetes. In fact, *KS* increased with the biomass of odontocetes and pinnipeds (nonsignificant), but not with the biomass of mysticetes (Figure 3b-d). We found no effect of consumption-biomass ratio (*QB*) and latitude on *KS*. Details on the validation of most parsimonious models can be found in SM2.

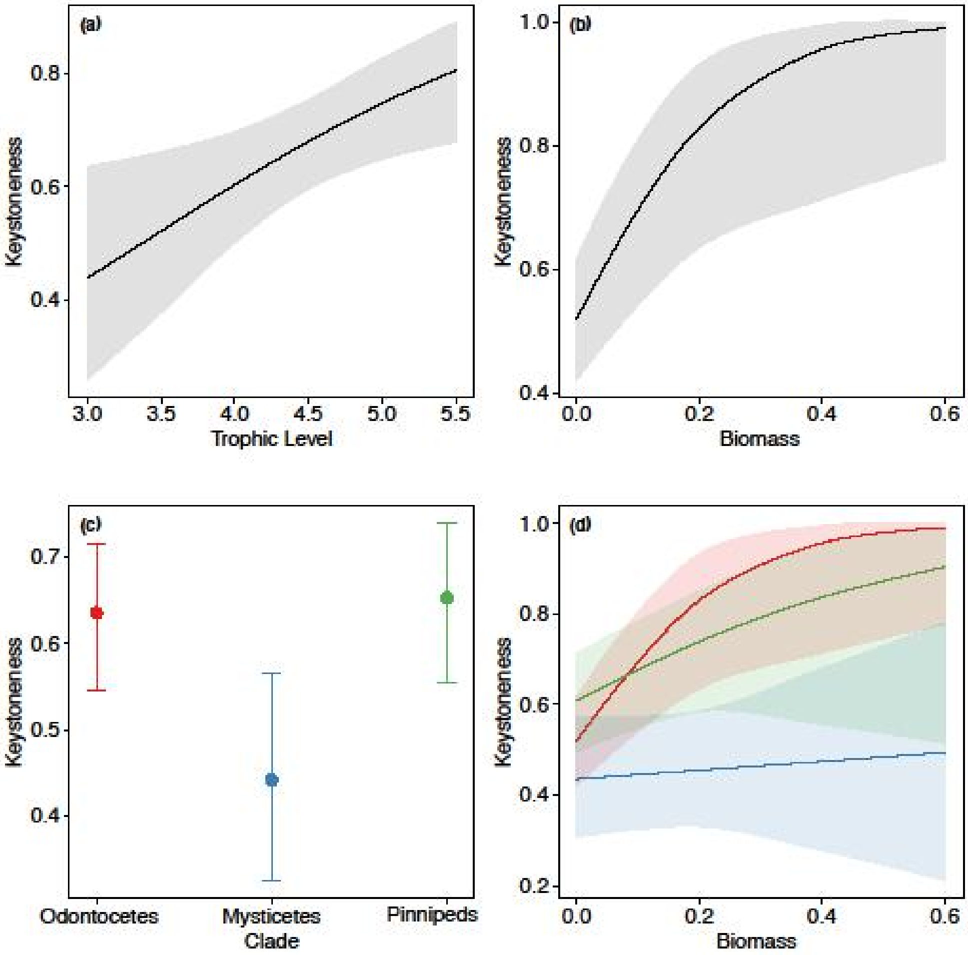

Fig. 3. **Keystoneness index as a function of trophic level, group biomass, clade, and biomass per clades**. Predicted effect of *TL* on Keystoneness index (*KS*) (a); Predicted effect of group biomass on *KS* (b); Predicted effect of clades on *KS* (c); Predicted effect of group biomass by clades on *KS* (red lines = odontocetes; blue lines = mysticetes; green lines = pinnipeds) (d). Shaded areas represent the 95% confidence interval of predicted values. All variables were taken from 157 marine mammal functional groups in 55 Ecopath models (see section 2.1). Points are predicted values. Bars represent the 95% confidence interval of predicted values.

DISCUSSION

Our results showed that the trophic impact (TI) increased at higher trophic levels (TL). We also found that TI increased as a function of the group biomass, but in this case, only for odontocetes and slightly for pinnipeds, with no effect for mysticetes, which also had the lowest TL and trophic impact of the three clades. The keystoneness index (KS) showed a similar pattern. There was a positive and significant relationship between KS and TL. Again, an increase in group biomass increased the keystoneness, but this relation was significant only for odontocetes. These findings confirm that the trophic position is the main factor affecting the predatory effects of marine mammals; for odontocetes and pinnipeds this impact was increased by the food intake of groups with high biomass/abundance. In contrast, we found no general effect of consumption/biomass ratio (QB) in trophic impact and keystoneness (despite a slight correlation for mysticetes), suggesting that variations in metabolic rate via body size—QB diminishes with body size—might not affect the predatory effects of marine mammals in the Ecopath models analysed. Finally, we found no latitudinal patterns in both the trophic impact and keystoneness, suggesting that the predatory effects of marine mammals are case dependent.

Ecopath models rely on species-specific diet information. Historically, an essential source of information on marine mammal diets has been stomach content analyses of dead animals (Ballance 2009). Other methods, such as faecal analysis, fatty acids, and stable isotopes, are now available to infer the diet of marine mammals; the complementary use of these methods is recommended to obtain the most informative results (Bowen & Iverson 2013). Unfortunately, our knowledge of the precise diet composition and consumption rates of marine mammals remains scarce in many cases. Given that our results were based only on outputs from balanced trophic models and that diet composition define the compartmental trophic positions—which in turn mediate the marine mammal predatory effects—further dietary studies for each population are needed to validate our conclusions and better understand the predatory effects of marine mammals within and across ecosystems. Even though balancing procedures during the construction of Ecopath models can help overcome gaps in diet information (Kavanagh et al. 2004), further implementations of Ecopath might provide tools to quantify potential autocatalytic loops and nutrient recycling (Lavery et al. 2014, Doughty et al. 2016, Veldhuis et al. 2018).

Identifying keystone species in food webs is critical for ecosystem conservation and management (Jordan 2009). Our results showed that one or more marine mammal functional groups were among the top three keystone groups in 32 out of the 55 (58%) Ecopath models assessed in our study. Therefore, decreasing marine mammal species abundance and biomass can affect biodiversity and the biomass of many components in marine communities (Power et al. 1996). We also found that TL correlated to our keystoneness index (KS3; Valls et al. 2015). mysticetes, however, feed on lower trophic levels than other marine mammal clades (Pauly et al. 1998), relying largely on zooplankton and pelagic shoaling fishes (Pivorunas 1979, Valenzuela et al. 2018). These shoaling fishes can connect many low trophic level species to higher ones in upwelling ecosystems and other environments, making them a key trophic group (Cury et al. 2000). It would be expected, therefore, that increased predation of mysticetes on pelagic fish might trigger a cascade effect in food webs of some ecosystems, increasing their interaction strength and supporting the hypothesis that baleen whales may play a vital role in some food webs, mainly in higher latitude marine ecosystems.

Furthermore, variation of both biomass and consumption rates affect energy-matter flux in ecosystems (Ulanowicz & Puccia 1990). Regarding TI, our results for mysticetes showed that QB dominated biomass, even though the trophic impacts of these large cetaceans were low compared to those of odontocetes and pinnipeds. This can be explained because many mysticetes import energy/matter in many ecosystems along with migration, and such imports can vary according to body size, reproductive status and time spent in the feeding grounds (Irvine et al. 2017). In contrast, biomass dominated over QB for the odontocetes. The trophic impact for mysticetes could be greater in their feeding grounds, generally in the higher latitudes—although we did not find an effect of latitude in TI. The smaller Odontocete biomasses correlate positively and significantly with TI; thus, the decline of the abundance of odontocetes could trigger significant changes in the communities they inhabit (Power et al. 1996). In addition to these findings, the movement of N, Fe, P, and other nutrients through whale excretion and defecation could play an important role in primary productivity at the surface and in deep-sea systems after death (Roman et al. 2014).

Metabolic rates have been used to measure the predatory effects of marine mammals (Morissete & Brodie 2014). However, we found no significant correlation between the QB ratio and the trophic impact and keystoneness (with the exception of mysticetes; but all mysticetes species can be categorized as being large-bodied marine mammals). Although metabolic rates may be useful to assess the predatory effects of marine mammals at the local scale, the use of holistic methods such as the trophic impact and keystone species indices seem a better choice for comparing the predatory effects of species across different ecosystems at the regional or larger scales. We concluded that the impact of a particular species in the food web context—in terms of its interaction strength—relies heavily on the type of prey a given predator is locally consuming, which can vary across ecosystems and affected by predator biomass and its food intake.

In our study, we did not detect, for any clade, trophic impact and keystoneness variations across latitudes. Marine mammal richness appears to be higher in temperate regions (Kaschner et al. 2006, Kaschner et al. 2011, Pompa et al. 2011), and previous studies proposed that marine mammal population size is positively associated with primary productivity (Pan et al. 2016). Indeed, our exploratory results showed that the total biomass is greater in higher latitudes, which tend to have more productive waters. This is likely due to variation detected for the biomass of the mysticetes, as the biomass of smaller marine mammals did not differ significantly across ecosystem types or along latitudinal gradients, although varied for mysticetes. Also, our results showed that the predatory effects of mysticetes appear not to be affected by biomass variations. However, we can fairly speculate about the likely predatory effects of baleen whales in the not-too-distant past (before whaling), when the abundance of some populations of baleen whales could have been several times larger than they are now (Roman & Palumbi 2003).

Our study showed that the higher the trophic level, the greater the trophic impact attribute is, and the higher the keystoneness rank. This happens because the higher the trophic level, the greater the probability of trophic cascades and indirect effects to occur throughout food webs (Abrams et al. 1996, Yodzis 2001, Estes 2009). The predatory effects of marine mammals can affect the entire ecosystem, and they can benefit fisheries through indirect effects on food webs (Gerber et al. 2009, Costalago et al. 2018, Gregr et al. 2020). Yet our results also give insights into the competition for food resources between fisheries and marine mammal through consumptive effects. The worldwide decline in the trophic level of fish populations through overfishing (Pauly 1998) could affect many marine mammals by reducing the availability of higher trophic level prey. Since odontocetes and pinnipeds feed on higher trophic levels, these two clades could be more vulnerable to food web perturbations.Recent models suggest that climate change could also amplify competition in higher trophic levels, raising concerns on the structure, function, and stability of ocean ecosystems (Lotze et al. 2019).

Our understanding of predatory effects is a first step in examining the ecological role of marine mammals, which also includes nutrient cycling, stranding and deadfall carbon, and trophic cascades (Roman et al. 2014, Roman & Estes 2017). Dead whales, for example, are the largest, most food-rich detrital particles in the ocean, often containing more than 106 g of organic carbon in energy-rich lipids and proteins (Smith 2006). These food-rich conditions, along with the widespread occurrence of whale falls have led to ecological and evolutionary opportunities on the deep-sea floor, in a manner similar to that of hydrothermal vents and cold seeps. By following these and other ecological pathways, we will have a fuller understanding of marine mammal ecology and be better placed to conduct ecosystem-based management of fisheries and other human activities in the ocean.

Availability of data and materials: The R code and data to reproduce the analyses can be made available upon request.

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Supplementary Material 1 for the article: The role of mammals as key predators in marine ecosystems

Table S1. Sellection of food web Ecopath models available that included marine mammals in their parameterization. Abbrevviations of ocean/sea are as follows: Arctic, ARC; Antarctic, ANT; Atlantic, ATL; Indian, IND; Pacific, PAC; and Mediterranean, MED. Ecosystem types are as follows: Arctic shelf, ARCS; Antarctic shelf, ARTS; Open Ocean, OCEAN; Temperate coastal and shelf areas, TEM; Tropical coastal and shelf areas, TROP; Coral Reefs, REEF and Upwelling ecosystems UPW. Years of modelling are recorded. Biomass (B, t·km-2), Production per unit of Biomass (P/B, y-1), Consumption per unit of Biomass (Q/B, y-1), Trophic Level (TL), Omnivory Index (OI), Relative Total Impact (TI), Keystoneness indices (KS1, KS2 and KS3), KS = KS3 Ranking/No. of trophic groups, Top-Down effect (TD%), and Mean Trophic Level of the Catch (MTL).

N	Ecopath group	Name group	Species aggregation	Group	Relative size	Location	Approximate latitude (Decimal degree)	Approximate longitude (Decimal degree)	Ocean	Ecosystem type	Year	No. of trophic groups (from Keystoneness table)	No. of trophic groups (including Detritus)	No. of fleets	Total No. of groups (from MTI dataset)	TL	B	P/B	Q/B	KS1 Score	KS2 Score	TI	KS3 Score	Ranking (ascending sort KS3)	KS	OI	TD (%)	MTL	Target group	Pedigree	DC Pedigree score	Reference
1	1	Killer whales	*Orcinus orca*	Odontocetes	Large	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	4,589	0,001	0,06	4,8	0,335	5,722	1	1,782	29	1	0,172	54,84	3,163	No	No	_	Bredesen 2003
1	2	Sperm whales	*Physeter macrocephalus*	Odontocetes	Large	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	4,698	0,009	0,065	4,2	-0,973	3,46	0,049	0,369	12	0,413793103	0,162	51,61	3,163	No	No	_	Bredesen 2003
1	3	Baleen whales	*Megaptera novaeangliae* , *Balaenoptera musculus* , *Balaenoptera physalus* , *Balaenoptera borealis* , *Eubalaena australis*	Mysticetes	Large	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	3,43	0,012	0,085	4,8	-1,096	3,213	0,037	0,227	5	0,172413793	0,159	74,19	3,163	No	No	_	Bredesen 2003
1	4	Minke whales	*Balaenoptera acutorostrata*	Mysticetes	Large	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	3,397	0,014	0,095	4,8	-0,861	2,38	0,067	0,285	8	0,275862069	0,081	61,29	3,163	No	No	_	Bredesen 2003
1	5	Small cetaceans	_	Odontocetes	_	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	4,456	0,049	0,15	7,2	-0,55	3,14	0,131	0,706	20	0,689655172	0,351	51,61	3,163	No	No	_	Bredesen 2003
1	6	Antarctic fur seals	*Arctocephalus gazella*	Pinnipeds	Small	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	3,862	0,032	0,15	3,197	-0,334	3,548	0,214	0,945	27	0,931034483	0,117	41,94	3,163	No	No	_	Bredesen 2003
1	7	Elephant seals	*Mirounga leonina*	Pinnipeds	Large	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	4,621	0,083	0,15	2,656	-0,675	2,794	0,098	0,502	15	0,517241379	0,109	61,29	3,163	No	No	_	Bredesen 2003
1	8	Crabeater Seals	*Lobodon carcinophagus*	Pinnipeds	Medium	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	3,41	0,005	0,11	5,798	-0,902	3,787	0,058	0,496	14	0,482758621	0,405	48,39	3,163	No	No	_	Bredesen 2003
1	9	Leopard Seals	*Hydrurga leptonyx*	Pinnipeds	Medium	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	4,099	0,001	0,15	5,343	0,0775	5,465	0,553	1,509	28	0,965517241	0,405	45,16	3,163	No	No	_	Bredesen 2003
1	10	Weddel and Ross Seals	*Leptonychotes weddelli* , *Ommatophoca rossii*	Pinnipeds	Medium	South Shetlands	-54,618327	-37,011119	ANT	OCEAN	1990s	29	30	1	30	4,26	0,00	0,22	11,38	-1,57	4,32	0,01	-0,11	2	0,068965517	0,22	67,74	3,163	No	No	_	Bredesen 2003
2	11	Baleen whales	*Balaenoptera physalus* , *Balaenoptera acutorostrata* , *Megaptera novaeangliae* , *Balaena mysticetus* , *E. japonica* , *Eschrichtius robustus*	Mysticetes	Large	Eastern Bering Sea	56,559501	-160,517422	PAC	OCEAN	1980s	23	25	1	26	3,67	0,39	0,02	11,38	-1,03	1,78	0,07	0,15	7	0,304347826	0,39	53,85	3,295	Yes	No	_	Trites et al. 1999
2	12	Toothed whales	*Delphinapterus leucas* , *Orcinus orca* , *Phocoenoides dalli* , *Phocoena phocoena*	Odontocetes	_	Eastern Bering Sea	56,559501	-160,517422	PAC	OCEAN	1980s	23	25	1	26	4,33	0,01	0,02	13,11	-0,29	4,16	0,38	1,03	23	1	0,23	46,15	3,295	Yes	No	_	Trites et al. 1999
2	13	Sperm whales	*Physeter macrocephalus*	Odontocetes	Large	Eastern Bering Sea	56,559501	-160,517422	PAC	OCEAN	1980s	23	25	1	26	4,71	0,21	0,02	4,55	-4,78	0,244	0,244	0,726	17	0,739130435	0,03	53,85	3,295	Yes	No	_	Trites et al. 1999
2	14	Beaked whales	*Stejnegers* spp.	Odontocetes	Medium	Eastern Bering Sea	56,559501	-160,517422	PAC	OCEAN	1980s	23	25	1	26	4,58	0,00	0,02	10,52	-1,626	3,783	0,017	-0,26	3	0,130434783	0,21	53,85	3,295	Yes	No	_	Trites et al. 1999
2	15	Walrus and bearded seals	*Odobenus rosmarus* , *Erignathus barbatus*	Pinnipeds	Medium	Eastern Bering Sea	56,559501	-160,517422	PAC	OCEAN	1980s	23	25	1	26	3,53	0,07	0,06	11,25	-0,87	2,67	0,10	0,37	9	0,391304348	0,29	61,54	3,295	Yes	No	_	Trites et al. 1999
2	16	Seals	*Callorhinus ursinus* , *Phoca vitulina* , *Phoca largha* , *Histriophoca fasciata* , *Pusa hispida*	Pinnipeds	_	Eastern Bering Sea	56,559501	-160,517422	PAC	OCEAN	1980s	23	25	1	26	3,95	0,07	0,06	15,93	-0,42	3,17	0,28	0,83	19	0,826086957	0,30	65,38	3,295	Yes	No	_	Trites et al. 1999
2	17	Steller sea lions	*Eumetopias jubatus*	Pinnipeds	Medium	Eastern Bering Sea	56,559501	-160,517422	PAC	OCEAN	1980s	23	25	1	26	4,24	0,02	0,06	12,70	-1,85	2,27	0,01	-0,55	2	0,086956522	0,04	69,23	3,295	Yes	No	_	Trites et al. 1999

N	Ecopath group	Name group	Species aggregation	Group	Relative size	Location	Approximate latitude (Decimal degree)	Approximate longitude (Decimal degree)	Ocean	Ecosystem type	Year	No. of trophic groups (from Keystoneness table)	No. of trophic groups (including Detritus)	No. of fleets	Total No. of groups (from MTI dataset)	TL	B	P/B	Q/B	KS1 Score	KS2 Score	TI	KS3 Score	Ranking (ascending sort KS3)	KS	OI	TD (%)	MTL	Target group	Pedigree	DC Pedigree score	Reference
3	18	Minke	*Balaenoptera acutorostrata*	Mysticetes	Large	Barents Sea	69,929021	33,725156	ARC	ARCS	1990s	38	41	6	47	4,3	0,159	0,035	9,9	-0,52	2,35	0,22	0,88	27	0,710526316	0,14	53,19	3,982	No	No	_	Blanchard et al. 2002
3	19	Other baleen whale	*Balaenoptera physalus* , *Megaptera novaeangliae*	Mysticetes	Large	Barents Sea	69,929021	33,725156	ARC	ARCS	1990s	38	41	6	47	4,30	0,112	0,02	12,89	-0,27	2,75	0,39	1,19	32	0,842105263	0,15	0,596	3,982	No	No	_	Blanchard et al. 2002
3	20	Toothed whales	*Phocoena phocoena* , *Lagenorhynchus albirostris* , *Orcinus orca*	Odontocetes	_	Barents Sea	69,929021	33,725156	ARC	ARCS	1990s	38	41	6	47	4,80	0,018	0,02	12,75	-2,16	3,61	0,45	1,35	35	0,921052632	0,19	46,81	3,982	No	No	_	Blanchard et al. 2002
3	21	Seals	*Pagophilus groenlandicus* , *Cystophora cristata, Phoca vitulina* , *Halichoerus grypus* , *Pusa hispida* , *Erignathus barbatus*	Pinnipeds	_	Barents Sea	69,929021	33,725156	ARC	ARCS	1990s	38	41	6	47	4,70	0,111	0,056	13,00	-0,10	2,93	0,58	1,37	36	0,947368421	0,20	53,19	3,982	No	No	_	Blanchard et al. 2002
4	22	Dolphins	_	Odontocetes	_	Azores	38,546358	-27,111199	ATL	OCEAN	1990s	44	45	11	56	4,31	0,00	0,10	11,41	-1,43	2,69	0,01	0,14	7	0,159090909	0,15	69,64	3,948	No	Yes	0,00	Morato et. al. 2016
4	23	Baleen whales	_	Mysticetes	_	Azores	38,546358	-27,111199	ATL	OCEAN	1990s	44	45	11	56	3,49	0,02	0,06	5,56	-1,87	1,20	0,00	-0,51	2	0,045454545	0,11	66,07	3,948	No	Yes	0,00	Morato et. al. 2016
4	24	Toothed whales	_	Odontocetes	_	Azores	38,546358	-27,111199	ATL	OCEAN	1990s	44	45	11	56	4,64	0,06	0,06	0,02	3,29	3,29	0,96	1,90	43	0,977272727	0,06	57,14	3,948	No	Yes	0,00	Morato et. al. 2016
5	25	Vaquita	*Phocoena sinus*	Odontocetes	Small	Alto Golfo de California	31,066392	-114,046112	PAC	TEM	1970s-2000s	28	29	3	32	4,13	0,00	0,60	30,00	-0,73	4,19	0,24	0,72	20	0,714285714	0,15	59,38	2,935	Yes	No	_	Morales-Zárate et al. 2004
5	26	Lobo marino	*Zalophus californianus*	Pinnipeds	Medium	Alto Golfo de California	31,066392	-114,046112	PAC	TEM	1970s-2000s	28	29	3	32	4,05	0,03	0,54	23,73	-0,32	3,26	0,62	0,62	27	0,964285714	0,08	53,13	2,935	Yes	No	_	Morales-Zárate et al. 2004
5	27	Ballenas dentadas	_	Odontocetes	_	Alto Golfo de California	31,066392	-114,046112	PAC	TEM	1970s-2000s	28	29	3	32	3,93	0,14	0,24	26,45	-0,12	2,83	0,96	1,20	28	1	0,03	56,25	2,935	No	No	_	Morales-Zárate et al. 2004
5	28	Ballenas barbadas	_	Mysticetes	_	Alto Golfo de California	31,066392	-114,046112	PAC	TEM	1970s-2000s	28	29	3	32	3,59	0,19	0,20	2,92	-0,55	2,27	0,36	0,73	21	0,75	0,05	53,13	2,935	No	No	_	Morales-Zárate et al. 2004
6	29	Baleen whales	*Physeter macrocephalus* , *Balenoptera acutorostrata* , *Balaenoptera borealis* , *Balaenoptera musculus* , *Balaenoptera physalus* , *Megaptera novaeangliae*	Odontocetes_Mystycetes	Large	Azores archipelago	38,546358	-27,111199	ATL	TEM	1990s	43	44	13	57	4,098	0,123	0,02	5,563	-0,0385	2,423	0,807	1,193	37	0,860465116	0,315	57,89	3,797	No	No	_	Guénette & Morato 2001
6	30	Dolphins	*Globicephala melas* , *Globicephala macrorhynchus* , *Hyperoodon ampullatus* , *Mesoplodon europaeus* , *Mesoplodon bidens* , *Ziphius cavirostris* , *Delphinus delphis* , *Stenella coeruleoalba* , *Stenella frontalis* , *Grampus griseus* , *Tursiops truncatus*	Odontocetes	_	Azores archipelago	38,546358	-27,111199	ATL	TEM	1990s	43	44	13	57	4,708	0,0044	0,07	11,41	-0,527	3,389	0,267	1,027	33	0,76744186	0,279	59,65	3,797	No	No	_	Guénette & Morato 2001
6	31	Killer whales	*Pseudorca crassidens*	Odontocetes	Large	Azores archipelago	38,546358	-27,111199	ATL	TEM	1990s	43	44	13	57	5,304	0,000063	0,02	10,27	-0,066	5,688	0,755	1,567	43	1	0,101	45,61	3,797	No	No	_	Guénette & Morato 2001
7	32	Dolphins	Delphinidae	Odontocetes	_	Baja California	25,83277	-112,761904	PAC	TROP	1970s	17	18	8	26	4,423	0,12	0,065	16,5	-1,229	1,693	0,082	-0,15	2	0,117647059	0,074	65,38	3,557	No	No	_	Cisneros-Montemayor et al. 2012
8	33	Sea otter	*Enhydra lutris*	Lutrinae	Small	Alaska, Prince William Sound	60,612852	-147,00572	PAC	TEM	1980s	18	19	1	20	3,303	0,017	0,71	92	-1,922	2,877	0,007	-0,72	4	0,222222222	0,324	30	3,739	No	No	_	Dalsgaard et al. 1997
8	34	Pinnipeds	*Phoca vitulina* , *Eumetopias jubatus*	Pinnipeds	Medium	Alaska, Prince William Sound	60,612852	-147,00572	PAC	TEM	1980s	18	19	1	20	4,549	0,3	0,06	29,1	-0,23	3,323	0,33	0,849	15	0,833333333	1,761	55	3,739	No	No	_	Dalsgaard et al. 1997
8	35	Resident mammals	*Orcinus orca* , *Phocoenoides dalli* , *Phocoena phocoena*	Odontocetes	Medium	Alaska, Prince William Sound	60,612852	-147,00572	PAC	TEM	1980s	18	19	1	20	4,413	0,095	0,02	12,1	-0,0172	4,035	0,538	1,129	17	0,944444444	0,242	65	3,739	No	No	_	Dalsgaard et al. 1997
8	36	Transient mammals	*Balaenoptera physalus* , *Megaptera novaeangliae* , *Balaenoptera acutorostrata* , *Delphinapterus leucas* , *Orcinus orca* occurring only seasonally in PWS.	Odontocetes_Mysticetes	_	Alaska, Prince William Sound	60,612852	-147,00572	PAC	TEM	1980s	18	19	1	20	3,988	0,28	0,02	3	0,252	3,835	0,538	1,129	18	1	0,174	45	3,739	No	No	_	Dalsgaard et al. 1997
9	37	Dauphins	_	Odontocetes	_	Bamboung, Senegal	14,541768	-17,444616	ATL	TROP	2000s	30	31	1	32	3,734	0,000475	0,07	12,12	-2,08	3,363	0,008	-0,6	1	0,033333333	0,069	59,38	2,704	No	No	_	Colléter et al. 2012
10	38	Striped dolphins	*S. coeruleoalba*	Odontocetes	Small	Bay of Biscay	47,024435	-3,026975	ATL	TEM	1994-2005	32	32	1	33	4,73	0,00585	0,08	20,797	-1,11	2,87	0,08	0,33	10	0,3125	0,84	48,48	3,756	Yes	Yes	1,00	Lassalle et al. 2011, Lassalle pers. comm
10	39	Bottlenose dolphins	*T. truncatus*	Odontocetes	Medium	Bay of Biscay	47,024435	-3,026975	ATL	TEM	1994-2005	32	32	1	33	5,18	0,0218	0,08	21,67	-0,30	3,10	0,48	1,08	31	0,96875	0,22	51,52	3,756	Yes	Yes	1,00	Lassalle et al. 2011, Lassalle pers. comm
10	40	Common dolphins	*D. delphis*	Odontocetes	Small	Bay of Biscay	47,024435	-3,026975	ATL	TEM	1994-2005	32	32	1	33	4,61	0,01443	0,08	26,115	-0,73	2,85	0,18	0,67	20	0,625	0,06	60,61	3,756	Yes	Yes	1,00	Lassalle et al. 2011, Lassalle pers. comm
10	41	Long-finned pilot whales	*G. melas*	Odontocetes	Large	Bay of Biscay	47,024435	-3,026975	ATL	TEM	1994-2005	32	32	1	33	4,64	0,00829	0,05	10,34	-1,16	2,67	0,07	0,26	6	0,1875	1,90	48,48	3,756	Yes	Yes	1,00	Lassalle et al. 2011, Lassalle pers. comm
10	42	Harbour porpoises	*P. phocoena*	Odontocetes	Small	Bay of Biscay	47,024435	-3,026975	ATL	TEM	1994-2005	32	32	1	33	4,68	0,00117	0,08	40,69	-1,77	2,91	0,02	-0,31	2	0,0625	0,06	51,52	3,756	Yes	Yes	1,00	Lassalle et al. 2011, Lassalle pers. comm
11	43	Odontocetae	_	Odontocetes	_	British Columbia coast	51,450086	-129,673838	PAC	TEM	1950-2000	52	53	21	74	4,718	0,036	0,03	13,1	-0,132	3,659	0,649	1,492	52	1	0,128	51,35	3,485	No	No	_	Preikshot 2007
11	44	Mysticetae	_	Mysticetes	_	British Columbia coast	51,450086	-129,673838	PAC	TEM	1950-2000	52	53	21	74	3,443	0,155	0,02	13,37	-1,011	2,145	0,086	0,056	25	0,480769231	0,328	59,46	3,485	No	No	_	Preikshot 2007
11	45	Sea lions	_	Pinnipeds	_	British Columbia coast	51,450086	-129,673838	PAC	TEM	1950-2000	52	53	21	74	4,582	0,019	0,06	12,7	-0,514	3,554	0,269	1,158	49	0,942307692	0,181	59,46	3,485	No	No	_	Preikshot 2007
11	46	Seals	_	Pinnipeds	_	British Columbia coast	51,450086	-129,673838	PAC	TEM	1950-2000	52	53	21	74	4,743	0,04	0,16	15,95	-0,282	3,463	0,458	1,331	51	0,980769231	0,206	56,76	3,485	No	No	_	Preikshot 2007
12	47	Mammals	*Tursiops* sp.; *Stenella* sp.; *Delphinus* sp.	Odontocetes_Mystyceti	_	Cape Verde	16,523711	-23,525301	ATL	TROP	1980s	30	31	3	34	4,303	0,03441031	0,1	11,79	-0,955	2,579	0,105	0,477	13	0,433333333	0,989	52,94	3,475	No	No	_	Stobberup et al. 2004
13	48	Minke whales	*Balaenoptera acutorostrata*	Mysticetes	Large	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	3,887	0,00453	0,099	8,4212	-2,372	2,323	0,004	-1,03	5	0,178571429	0,707	43,33	3,281	No	No	_	Melgo et al. 2009
13	49	Fin whales	*Balaenoptera physalus*	Mysticetes	Large	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	3,215	0,00618	0,099	4,1608	-5,096	-0,54	7E-06	-3,77	2	0,071428571	0,397	46,67	3,281	No	No	_	Melgo et al. 2009
13	50	Humpback whales	*Megaptera novaeangliae*	Mysticetes	Large	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	3,739	0,0696	0,099	5,0808	-2,002	1,507	0,008	-0,96	6	0,214285714	0,639	70	3,281	No	No	_	Melgo et al. 2009
13	51	Brydes whales	*Balaenoptera brydei*	Mysticetes	Large	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	3,857	0,00432	0,05	6,26	-1,158	3,558	0,059	0,204	12	0,428571429	0,378	46,67	3,281	No	No	_	Melgo et al. 2009
13	52	Sei whales	*Balaenoptera borealis*	Mysticetes	Large	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	3,217	0,00085	0,02	6,1776	-5,075	0,347	7E-06	-3,68	3	0,107142857	0,4	43,33	3,281	No	No	_	Melgo et al. 2009
13	53	Blue whales	*Balaenoptera musculus*	Mysticetes	Large	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	3,20	0,00	0,06	3,40	-5,83	-0,87	0,00	-4,45	1	0,035714286	0,39	6,667	3,281	No	No	_	Melgo et al. 2009
13	54	Sperm whales	*Physeter macrocephalus*	Odontocetes	Large	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	4,24	0,02	0,05	5,03	-1,98	2,09	0,01	-0,73	7	0,25	0,01	56,67	3,281	No	No	_	Melgo et al. 2009
13	55	Killer whales	*Orcinus orca*	Odontocetes	Large	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	4,07	0,00	0,02	9,47	-0,17	5,46	0,57	1,24	28	1	0,31	43,33	3,281	No	No	_	Melgo et al. 2009
13	56	Beaked whales	*Mesoplodon densirostris, M. europaeus, Ziphius caviostris*	Odontocetes	_	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	3,88	0,00	0,04	9,93	-3,37	2,87	0,00	-1,92	4	0,142857143	0,29	56,67	3,281	No	No	_	Melgo et al. 2009
13	57	Small cetaceans	*Delphinus delphis* , *Feresa attenuate* , *Globicephala macrorhynchus* , *Grampus griseus* , *Kogia breviceps* , *Kogia simus* , *Lagenodelphis hosei* , *Peponocephala electra* , *Pseudorca crassidens* , *Sousa teuszii* , *Stenella attenuate* , *Stenella clymene* , *Stenella coeruleoalba* , *Stenella frontalis* , *Stenella longisrostris* , *Steno bredanensis* , *Tursiops truncatus*	Odontocetes	_	Caribbean	18,007723	-69,756805	ATL	TROP	1980s	28	29	2	31	3,80	0,04	0,03	14,40	-0,48	3,27	0,28	0,67	22	0,785714286	0,33	63,33	3,281	No	No	_	Melgo et al. 2009

N	Ecopath group	Name group	Species aggregation	Group	Relative size	Location	Approximate latitude (Decimal degree)	Approximate longitude (Decimal degree)	Ocean	Ecosystem type	Year	No. of trophic groups (from Keystoneness table)	No. of trophic groups (including Detritus)	No. of fleets	Total No. of groups (from MTI dataset)	TL	B	P/B	Q/B	KS1 Score	KS2 Score	TI	KS3 Score	Ranking (ascending sort KS3)	KS	OI	TD (%)	MTL	Target group	Pedigree	DC Pedigree score	Reference
14	58	Baleen whales	_	Mysticetes	_	Celtic Sea (France, UK, Irlande)	49,863987	-9,769045	ATL	TEM	1980s	46	48	18	66	3,98	0,07	0,04	4,77	-1,01	2,18	0,09	0,54	21	0,456521739	0,22	54,55	3,427	No	No	_	Moullec et al. 2017
14	59	Toothed whales	_	Odontocetes	_	Celtic Sea (France, UK, Irlande)	49,863987	-9,769045	ATL	TEM	1980s	46	48	18	66	4,63	0,03	0,14	12,00	-0,31	3,183	0,464	1,32	46	1	0,08	62,12	3,427	No	No	_	Moullec et al. 2017
15	60	Baleen whales	*Balaenoptera acutorostrata* , *Balaenoptera borealis* , *Balaenoptera edeni* , *Balaenoptera musculus* , *Balaenoptera physalus* , *Eubalaena glacialis* , *Megaptera novaeangliae*	Mysticetes	Large	Central Atlantic	3,218475	-27,500191	ATL	OCEAN	1950s	37	38	1	39	4,03	0,04	0,02	4,39	-1,89	1,70	0,01	-0,59	4	0,108108108	0,10	69,23	4,023	No	No	_	Vasconcellos & Watson 2004
15	61	Toothed whales	*Delphinapterus leucas* , *Delphinus delphis* , *Feresa attenuata* , *Globicephala macrorhynchus* , *Globicephala melas* , *Grampus griseus* , *Kogia breviceps* , *Kogia simus* , *Lagenodelphis hosei* ,	Odontocetes	_	Central Atlantic	3,218475	-27,500191	ATL	OCEAN	1950s	37	38	1	39	5,02	0,08	0,02	6,69	0,06	3,37	0,92	1,29	33	0,891891892	0,27	56,41	4,023	No	No	_	Vasconcellos & Watson 2004
15	62	Beaked whales	Ziphiidae: *Hyperoodon ampullatus* , *Mesoplodon bidens* , *Mesoplodon densirostris* , *Mesoplodon europaeus* , *Mesoplodon mirus* , *Ziphius cavirostris*	Odontocetes	_	Central Atlantic	3,218475	-27,500191	ATL	OCEAN	1950s	37	38	1	39	4,87	0,00	0,02	8,81	-0,99	4,26	0,08	0,52	14	0,378378378	0,29	56,41	4,023	No	No	_	Vasconcellos & Watson 2004
16	63	Seals	*Halichoerus grypus*	Pinnipeds	Medium	Central Baltic Sea	56,52278	19,251778	ATL	TEM	1970s	20	22	3	25	4,58	0,00	0,10	12,77	-2,29	2,82	0,01	-0,99	2	0,1	1,28	64,00	3,43	No	No	_	Tomczak et al. 2012
17	64	Sea Lion	*Otaria flavescens*	Pinnipeds	Medium	Central Chile	-35,804754	-72,970047	PAC	UPW	1990s	20	21	1	22	3,90	0,05	1,05	15,00	-0,92	2,97	0,09	0,36	11	0,55	0,63	45,45	2,42	No	No	_	Neira et al. 2004
18	65	Sea mammals	_	_	_	Central Gulf of California, Mexico	27,54636	-111,130632	PAC	TEM	1970s	25	27	4	31	4,00	0,02	2,17	29,30	-1,09	2,57	0,07	0,29	8	0,32	0,26	0,52	2,99	No	No	_	Arreguín-Sánchez et al., 2002
19	66	Baleen whales	_	Mysticetes	_	Denmark, Faroe Islands	61,913209	-6,699613	ATL	OCEAN	1990s	19	20	13	33	3,98	0,06	0,05	5,06	-1,27	2,07	0,06	-0,01	5	0,263157895	0,31	48,48	3,723	No	No	_	Zeller & Reinert 2004
19	67	Toothed mammals	*Globicephala melas, Lagenorhynchus acutus*	Odontocetes	_	Denmark, Faroe Islands	61,913209	-6,699613	ATL	OCEAN	1990s	19	20	13	33	4,67	0,09	0,05	12,27	-0,25	2,93	0,63	0,98	19	1	0,16	51,52	3,723	No	No	_	Zeller & Reinert 2004
20	68	Predatory marine mammals	_	_	_	Galapagos, Ecuador	-0,888058	-90,564199	PAC	REEF	2000s	32	33	4	37	3,64	86,98	0,24	4,71	-0,10	3,59	0,27	1,38	32	1	0,84	32,43	3,015	No	No	_	Ruiz et al. 2016
20	69	Dolphins	_	Odontocetes	_	Galapagos, Ecuador	-0,888058	-90,564199	PAC	REEF	2000s	32	33	4	37	3,60	0,20	0,04	16,13	-1,85	1,82	0,00	-0,39	3	0,09375	0,57	64,86	3,015	No	No	_	Ruiz et al. 2016
21	70	Toothed cetaceans	_	Odontocetes	_	Galapagos, Floreana rocky reef, Ecuador	-1,231546	-89,394988	PAC	REEF	2000s	42	43	1	44	4,41	0,02	0,08	14,60	-0,49	4,57	0,14	1,13	32	0,761904762	0,50	47,73	2,272	No	No	_	Okey et al. 2004
21	71	Sea lions	*Zalophus wollebaeki*	Pinnipeds	Medium	Galapagos, Floreana rocky reef, Ecuador	-1,231546	-89,394988	PAC	REEF	2000s	42	43	1	44	4,01	5,68	0,07	25,55	0,34	3,00	0,92	1,75	41	0,976190476	1,27	52,27	2,272	No	No	_	Okey et al. 2004
22	72	Baleen whales	*Balaenoptera acutorostrata* , *B. borealis* , *B. edeni* , *B. musculus* , *B. physalus* , *Megaptera novaeangliae*	Mysticetes	Large	Sierra Leone	7,506951	-13,425644	ATL	TROP	1990s	43	44	2	46	3,935	0,03	0,02	4,85	-0,82	2,40	0,11	0,64	22	0,511627907	0,10	69,57	3,061	No	No	_	Heymans & Vakily 2004
22	73	Toothed whales and dolphins	*Kogia breviceps* , *K. simus* , *Physeter macrocephalus* , *Mesoplodon europaeus* , *Ziphius carvirostris* , *Feresa attenuata* , *Globicephala macrorhynchus* , *Orcinus orca* , *Peponocephala electra* , *Psuedorca crassidens* , *Delphinus delphis* , *Sousa teuszii* , *Stenella coeruleoalba* , *S. clymene* , *S. longirostris* , *S. attenuata* , *S. frontalis* , *Steno bredanensis* , *Tursiops truncatus* , *Grampus griseus*	Odontocetes	_	Sierra Leone	7,506951	-13,425644	ATL	TROP	1990s	43	44	2	46	4,691	0,06	0,07	14,55	-0,28	2,64	0,40	1,05	31	0,720930233	0,25	54,35	3,061	No	No	_	Heymans & Vakily 2004
23	74	Seals	*Arctocephalus pusillus pusillus*	Pinnipeds	Medium	South Benguela, South Africa	-32,078993	17,303118	ATL	TEM	1970s	31	32	13	45	4,74	0,07	0,25	19,31	-0,54	2,64	0,25	0,89	28	0,903225806	0,25	82,22	3,737	No	No	_	Shannon et al. 2003
23	75	Cetaceans	*Balaenoptera brydei*, other species	Odontocetes_Mystyceti	_	South Benguela, South Africa	-32,078993	17,303118	ATL	TEM	1970s	31	32	13	45	4,62	0,02	0,15	10,00	-0,54	2,58	0,12	0,60	17	0,548387097	0,15	60	3,737	No	No	_	Shannon et al. 2003
24	76	Whales and porpoises	*Balaenoptera physalus* , *Balaenoptera acutorostrata* , *Megaptera novaeangliae* , *Phocoena phocoena* , *Lagenorhynchus acutus* , *Lagenorhynchus albirostris*	Odontocetes_Mystyceti	_	Southern Gulf of St. Lawrence, Canada	46,764781	-62,88142	ATL	TEM	1980s	29	30	1	31	4,25	0,02	0,09	10,00	-0,48	3,68	0,32	0,92	23	0,793103448	0,03	67,74	3,689	No	No	_	Savenkoff et al. 2007
24	77	Harp seals	*Pagophilus groenlandicus*	Pinnipeds	Medium	Southern Gulf of St. Lawrence, Canada	46,764781	-62,88142	ATL	TEM	1980s	29	30	1	31	4,04	0,23	0,03	3,31	-0,32	2,77	0,46	0,98	27	0,931034483	0,18	61,29	3,689	No	No	_	Savenkoff et al. 2007
24	78	Hooded seals	*Cystophora cristata*	Pinnipeds	Medium	Southern Gulf of St. Lawrence, Canada	46,764781	-62,88142	ATL	TEM	1980s	29	30	1	31	4,39	0,00	0,08	9,55	-0,49	4,48	0,31	0,95	25	0,862068966	0,09	48,39	3,689	No	No	_	Savenkoff et al. 2007
24	79	Grey seals	*Halichoerus grypus*	Pinnipeds	Medium	Southern Gulf of St. Lawrence, Canada	46,764781	-62,88142	ATL	TEM	1980s	29	30	1	31	4,51	0,03	0,07	7,13	-0,43	3,55	0,36	0,95	24	0,827586207	0,16	51,61	3,689	No	No	_	Savenkoff et al. 2007
24	80	Harbour seals	*Phoca vitulina*	Pinnipeds	Small	Southern Gulf of St. Lawrence, Canada	46,764781	-62,88142	ATL	TEM	1980s	29	30	1	31	4,32	0,00	0,05	5,21	-1,35	4,03	0,04	0,12	5	0,172413793	0,12	67,74	3,689	No	No	_	Savenkoff et al. 2007
25	81	baleen whales	*Eubalaena australis* , *Caperea marginata* , *Balaenoptera musculus* , *Balaenoptera physalus* , *Balaenoptera borealis* , *Balaebiotera acutorostrata* , *Megaptera novaeangliae*	Mysticetes	Large	Falkland Islands (Malvinas)	-51,657731	-59,326108	ATL	OCEAN	1990s	43	44	1	45	3,818	0,00	0,11	4,43	-3,76	2,80	0,00	-2,13	2	0,046511628	0,34	57,78	3,734	No	No	_	Cheung & Pitcher 2005
25	82	toothed whales	*Physeter catodon* , *Berardius arnuxii* , *Ziphius cavirostris* , *Hyperoodon planifrons* , *Mesoplodon grayi* , *Mesoplodon hectori* , *Mesoplodon layardii* , *Orcinus orca* , *Globicephala melas* , *Lagenorphynchus australis* , *Lagenorhynchus obscurus* , *Lagenorhynchus cruciger* , *Grampus griseus* , *Tursiops layardii* , *Lissodelphis peronii* , *Cephalorphynchus commersonii* , *Australophocaena dioptrica*	Odontocetes	_	Falkland Islands (Malvinas)	-51,657731	-59,326108	ATL	OCEAN	1990s	43	44	1	45	4,612	0,00	0,05	5,49	-1,80	4,16	0,01	-0,19	4	0,093023256	0,21	48,89	3,734	No	No	_	Cheung & Pitcher 2005
25	83	seals and sea lions	*Otaria byronia* , *Arctocephalus australis* , *Mirounga leonine* , *Lobodon carcinophagus* , *Lobodon carcinophagus*	Pinnipeds	_	Falkland Islands (Malvinas)	-51,657731	-59,326108	ATL	OCEAN	1990s	43	44	1	45	4,30	0,01	0,14	14,23	0,04	4,75	0,69	1,18	42	0,976744186	0,44	60	3,734	No	No	_	Cheung & Pitcher 2005
26	84	Dolphins	*T. truncatus*	Odontocetes	Medium_sized	Golfo Dulce, Costa Rica	8,432829	-83,170458	PAC	TROP	1990s	20	21	1	22	4,31	0,01	0,05	28,00	-0,45	2,57	0,46	0,85	18	0,9	0,18	45,45	4,266	No	No	_	Wolff et al. 1996
27	85	pinnipeds	_	Pinnipeds	_	Humboldt Current, Peru	-9,835408	-79,140433	PAC	UPW	1990s	32	33	1	34	3,45	0,07	0,10	45,90	-0,89	2,73	0,09	0,49	15	0,46875	0,06	50	2,617	No	No	_	Tam et al. 2008
27	86	cetaceans	_	Odontocetes_Mystyceti	_	Humboldt Current, Peru	-9,835408	-79,140433	PAC	UPW	1990s	32	33	1	34	4,25	0,06	0,10	20,00	-0,19	3,50	0,46	1,22	30	0,9375	0,47	29,41	2,617	No	No	_	Tam et al. 2008
28	87	Baleen whales	*Balaenoptera musculus* , *Balaena mysticetus* , *Balaenoptera physalus* , *Megaptera novaeangliae* , *Balaenoptera acutorostrata* , *Balaenoptera borealis*	Mysticetes	Large	Greenland, West Coast	68,415852	-54,419311	ARC	OCEAN	1990s	21	22	4	26	3,80	0,46	0,03	4,00	-0,76	1,78	0,19	0,32	13	0,619047619	0,48	46,15	3,158	No	No	_	Pedersen and Zeller 2001
28	88	Toothed whales	*Lagenorhynchus obliquidens* , *Hyperoodon ampullatus* , *Phocoena phocoena* , *Orcinus orca* , *Monodon monoceros* , *Globicephala melaena* , *Physeter macrocephalus* , *Lagenorhynchus albirostris* , *Delphinapterus leucas*	Odontocetes	_	Greenland, West Coast	68,415852	-54,419311	ARC	OCEAN	1990s	21	22	4	26	4,40	0,05	0,06	10,00	-0,56	2,95	0,29	0,64	16	0,761904762	0,64	61,54	3,158	No	No	_	Pedersen and Zeller 2001
28	89	Seals	*Erignathus barbatus* , *Phoca vitulina* , *Phoca groenlandica* , *Cystophora cristata* , *Phoca hispida* , *Odobenus rosmarus*	Pinnipeds	_	Greenland, West Coast	68,415852	-54,419311	ARC	OCEAN	1990s	21	22	4	26	4,32	0,51	0,07	15,00	-0,03	2,46	1,00	0,97	20	0,952380952	0,79	57,69	3,158	No	No	_	Pedersen and Zeller 2001
29	90	Baleines	*Balaenoptera physalus* , *Balaenoptera edeni* , *Balenoptera acutorostrata*	Mysticetes	Large	Guinea	9,880196	-14,311731	ATL	OCEAN	1990s	43	44	2	46	3,98	0,03	0,02	4,65	-1,00	2,65	0,08	0,57	21	0,488372093	0,12	52,17	3,246	No	No	_	Guénette & Diallo 2004
29	91	Dauphins	*Globicephala macrorhynchus* , *Delphinus delphis* , *Sousa teuszii* , *Stenella coeruleoalba* , *Stenella clymene* , *Stenella longisrostris* , *Stenella attenuata* , *Stenella longisrostris* , *Stenella attenuata* , *Stenella frontalis* , *Steno bredanensis* , *Tursiops truncatus*	Odontocetes	_	Guinea	9,880196	-14,311731	ATL	OCEAN	1990s	43	44	2	46	4,72	0,06	0,07	12,12	-0,42	2,93	0,30	0,98	34	0,790697674	0,25	43,48	3,246	No	No	_	Guénette & Diallo 2004
30	92	Odontocetes	*Tursiops truncatus* , *Delphinus delphis*	Odontocetes	_	Gulf of California, Mexico	29,35815	-112,666973	PAC	TEM	1990s	33	34	9	43	3,93	0,17	0,24	26,45	0,43	3,41	0,78	1,66	33	1	0,05	62,79	2,76	No	No	_	Lercari & Arreguín-Sánchez 2009
30	93	Phocoena sinus	*Phocoena sinus*	Odontocetes	Small	Gulf of California, Mexico	29,35815	-112,666973	PAC	TEM	1990s	33	34	9	43	3,92	0,00	0,60	30,00	-0,53	4,51	0,09	0,97	29	0,878787879	0,09	62,79	2,76	No	No	_	Lercari & Arreguín-Sánchez 2009
30	94	Mysticetes	*Balaenoptera physalus* , *Balaenoptera edeni*	Mysticetes	Large	Gulf of California, Mexico	29,35815	-112,666973	PAC	TEM	1990s	33	34	9	43	3,55	0,09	0,20	2,92	-1,66	1,60	0,01	-0,34	2	0,060606061	0,09	72,09	2,76	No	No	_	Lercari & Arreguín-Sánchez 2009

N	Ecopath group	Name group	Species aggregation	Group	Relative size	Location	Approximate latitude (Decimal degree)	Approximate longitude (Decimal degree)	Ocean	Ecosystem type	Year	No. of trophic groups (from Keystoneness table)	No. of trophic groups (including Detritus)	No. of fleets	Total No. of groups (from MTI dataset)	TL	B	P/B	Q/B	KS1 Score	KS2 Score	TI	KS3 Score	Ranking (ascending sort KS3)	KS	OI	TD (%)	MTL	Target group	Pedigree	DC Pedigree score	Reference
31	95	Dolphins	*Tursiops truncatus*	Odontocetes	Medium	Portofino, Italie	44,295756	9,196888	MED	TEM	2007-2014	32	33	3	36	4,95	0,03	0,07	13,49	-1,45	3,76	0,03	0,06	4	0,125	2,05	41,67	3,262	No	Yes	1,00	Prato et al. 2016
32	96	orque	*Orcinus orca*	Odontocetes	Large	Mauritania	18,64371	-16,386941	ATL	OCEAN	1980s	37	38	1	39	4,20	0,00	0,02	7,58	-2,17	4,12	0,00	-0,60	1	0,027027027	0,26	46,15	3,314	No	No	_	Ould Taleb Ould Sidi & Guénette 2004
32	97	dauphins	*Tursiops truncatus* , *Souza teuszii*	Odontocetes	Medium	Mauritania	18,64371	-16,386941	ATL	OCEAN	1980s	37	38	1	39	4,07	0,03	0,06	13,42	-0,97	2,82	0,08	0,55	15	0,405405405	0,157	51,28	3,314	No	No	_	Ould Taleb Ould Sidi & Guénette 2004
33	98	Baleen Whales	*Balaenoptera musculus* , *Balaenoptera edeni*	Mysticetes	Large	Eastern Tropical Pacific	2,255811	-98,059362	PAC	OCEAN	1990s	38	39	5	44	3,81	0,0091	0,02	9,10	-1,28	2,98	0,04	0,14	3	0,078947368	0,09	81,82	4,685	No	No	_	Olson & Watters 2003
33	99	Toothed Whales	*Tursiops* , *Grampus* , *Steno* , *Globicephala* , *Peponocephala* , *Feresa* , *Pseudorca* , *Orcinus* , *Zyphius* , *Mesoplodon* , *Kogia* , *Physeter*	Odontocetes	_	Eastern Tropical Pacific	2,255811	-98,059362	PAC	OCEAN	1990s	38	39	5	44	5,22	0,031	0,02	6,75	0,12	2,67	1,00	1,17	32	0,842105263	0,17	50,00	4,69	No	No	_	Olson & Watters 2003
33	100	Spotted Dolphin	*Stenella attenuata*	Odontocetes	Small	Eastern Tropical Pacific	2,255811	-98,059362	PAC	OCEAN	1990s	38	39	5	44	5,03	0,0035	0,04	16,50	-1,07	2,43	0,06	0,23	13	0,342105263	0,25	56,82	4,69	No	No	_	Olson & Watters 2003
33	101	Meso Dolphin	*Stenella longirostris* , *Stenella, coeruleoalba* , *Delphinus delphis* , *Lagenodelphis hosei* , *Lagenorhynchus obliquidens*	Odontocetes	_	Eastern Tropical Pacific	2,255811	-98,059362	PAC	OCEAN	1990s	38	39	5	44	4,65	0,017	0,04	16,50	-1,16	1,65	0,05	-0,05	10	0,263157895	0,20	56,82	4,69	No	No	_	Olson & Watters 2003
34	102	Whales	*Balaenoptera physalus, Balaenoptera edeni, Balenoptera acutorostrata*	Mysticetes	Large	Guinea	9,880196	-14,311731	ATL	TROP	2000s	34	35	2	37	4,01	0,03	0,02	4,65	-1,65	2,20	0,02	-0,14	6	0,176470588	0,06	62,16	3,233	No	No	_	Gascuel et al. 2009
34	103	Dolphins	*Globicephala macrorhynchus, Delphinus delphis, Sousa teuszii, Stenella coeruleoalba, Stenella clymene, Stenella longisrostris, Stenella attenuata, Stenella longisrostris, Stenella attenuata, Stenella*	Odontocetes	_	Guinea	9,880196	-14,311731	ATL	TROP	2000s	34	35	2	37	4,48	0,04	0,07	12,12	-0,73	2,97	0,19	0,76	29	0,852941176	0,33	48,65	3,233	No	No	_	Gascuel et al. 2009
35	104	marine mammals	*Otaria bryonia* , *Arctocephalus australis*	Pinnipeds	_	Sechura Bay, Peru	-5,589187	-81,054827	PAC	UPW	1990s	20	21	1	22	3,34	0,02	0,10	46,18	-0,90	3,64	0,14	0,38	12	0,6	0,12	50	2,146	No	No	_	Taylor et al. 2008
36	105	Mammiferes mari	*Balaenoptera physalus* , *Balaenoptera edeni* , dolphins, other whales	Odontocetes_Mystyceti	_	Senegal,Gambia	13,597271	-16,912022	ATL	UPW	1990s	16	18	2	20	3,341	0,039	0,047	17,265	-1,426	2,418	0,049	-0,22	3	0,1875	0,364	70	2,771	No	No	_	Samb & Mendy 2004
37	106	Mammals	_	_	_	West Coast of Peninsular Malaysia, Malaysia	4,481926	100,085828	PAC	TROP	1970s	14	15	1	16	4,89	0,02	0,05	30	-0,215	3,067	0,788	0,931	14	1	0,347	37,5	3,243	No	No	_	Christensen et al. 2003
38	107	Dolphin	*Tursiops truncatus*	Odontocetes	Medium	Gulf of Mexico, Mexico	28,37998	-90,599879	ATL	TROP	1980s	14	15	1	16	3,98	0,02	0,02	0,1	-1,118	2,123	0,07	-0	3	0,214285714	0,197	68,75	2,602	No	No	_	Browder 1993
39	108	Pinnipeds	_	Pinnipeds	_	Gulf of Maine, United States of America	42,469498	-70,045949	ATL	TEM	1990s	29	31	1	32	4,555	0,063	0,067	4,85	-0,499	2,852	0,326	0,881	26	0,896551724	0,128	59,38	3,579	No	No	_	Link et al. 2006
39	109	Baleen Whales	_	Mysticetes	_	Gulf of Maine, United States of America	42,469498	-70,045949	ATL	TEM	1990s	29	31	1	32	3,584	0,602	0,042	2,3	-1,55	0,822	0,029	-0,29	1	0,034482759	0,1	62,5	3,579	No	No	_	Link et al. 2006
39	110	Odontocetes	_	Odontocetes	_	Gulf of Maine, United States of America	42,469498	-70,045949	ATL	TEM	1990s	29	31	1	32	4,651	0,0336	0,04	8,5	-0,772	2,852	0,174	0,626	20	0,689655172	0,148	65,63	3,579	No	No	_	Link et al. 2006
40	111	Marine mammals	_	_	_	Icelandic shelf, Iceland	63,593744	-17,342317	ATL	OCEAN	1990s	20	21	1	22	3,503	1,745	0,01	5	0,03	2,171	1	0,936	19	0,95	0,311	59,09	3,043	No	No	_	Mendy & Buchary 2001
41	112	Mamiferos marin	*Delphinus delphis* , *Stenella atenuata* , *S. longirostris*	Odontocetes	Small	Jalisco and Colima Coast, Mexico	18,664671	-104,229571	PAC	TROP	1990s	36	38	3	41	4,098	0,338	3,086	12,543	-0,538	2,286	0,26	0,954	34	0,944444444	0,57	48,78	2,521	No	No	_	Galván Piña 2005
42	113	Baleen whales	*Balaena glacialis* , *Eschrichtius robustus* , *Balaenoptera acutorostrata* , *Balaenoptera physalus* , *Megaptera novaeangliae*	Mysticetes	Large	Western Bering Sea, Russian federation	59,756599	165,394672	PAC	TEM	1980s	33	36	1	37	3,774	0,391	0,02	8,312	-0,693	2,47	0,174	0,586	22	0,666666667	0,342	56,76	3,572	No	No	_	Aydin et al. 2002
42	114	Toothed whales	*Orcinus orca* , *Delphinapterus leucas* , *Phocoenoides dalli* , *Phocoena phocoena*	Odontocetes	_	Western Bering Sea, Russian federation	59,756599	165,394672	PAC	TEM	1980s	33	36	1	37	4,155	0,042	0,02	17,5	0,0667	4,198	1	1,529	33	1	0,94	37,84	3,572	No	No	_	Aydin et al. 2002
42	115	Sperm whales	*Physeter macrocephalus*	Odontocetes	Large	Western Bering Sea, Russian federation	59,756599	165,394672	PAC	TEM	1980s	33	36	1	37	4,703	0,02	0,02	9,8	-0,924	3,53	0,102	0,581	21	0,636363636	0,009	51,35	3,572	No	No	_	Aydin et al. 2002
42	116	Walrus& bearded seals	*Odobenus rosmarus divergens* , *Erignathus barbatus*	Pinnipeds	Medium	Western Bering Sea, Russian federation	59,756599	165,394672	PAC	TEM	1980s	33	36	1	37	3,151	0,262	0,06	13,9	-0,445	2,892	0,308	0,878	27	0,818181818	0,093	59,46	3,572	No	No	_	Aydin et al. 2002
42	117	Seals	*Callorhinus ursinus* , *Phoca vitulina* , *Phoca larga* , *Phoca fasciata* , *Phoca hispida*	Pinnipeds	_	Western Bering Sea, Russian federation	59,756599	165,394672	PAC	TEM	1980s	33	36	1	37	3,915	0,097	0,06	13,34	-0,111	3,657	0,664	1,269	32	0,96969697	1,122	45,95	3,572	No	No	_	Aydin et al. 2002
42	118	Steller sea lions	*Eumetopias jubatus*	Pinnipeds	Medium	Western Bering Sea, Russian federation	59,756599	165,394672	PAC	TEM	1980s	33	36	1	37	3,99	0,035	0,06	18	-0,384	3,826	0,354	1,107	31	0,939393939	1,069	56,76	3,572	No	No	_	Aydin et al. 2002
43	119	M. mammals	_	_	_	Gulf of Thailand, Thailand	11,570431	100,793909	PAC	TROP	1960s	28	29	2	31	4,883	0,025	0,05	30	-0,0108	3,542	0,77	1,387	28	1	0,063	45,16	3,009	No	No	_	Christensen 1993
44	120	Polar Bear WHB	*Ursus maritimus*	Ursoidae	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	4,857	0,000460363	0,129	2,08	-0,612	4,461	0,275	0,919	32	0,842105263	0,307	42,59	3,927	No	No	_	Hoover, 2010
44	121	SH Polar Bear	*Ursus maritimus*	Ursoidae	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	4,906	0,000383636	0,154	2,08	-0,485	4,668	0,368	1,059	34	0,894736842	0,211	59,26	3,927	No	No	_	Hoover 2010
44	122	Polar Bear Foxe	*Ursus maritimus*	Ursoidae	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	4,927	0,000191818	0,12	2,08	-0,67	4,783	0,24	0,886	31	0,815789474	0,163	40,74	3,927	No	No	_	Hoover 2010
44	123	Killer Whale	*Orcinus orca*	Odontocetes	Large	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	4,872	2,50E-05	0,151	4,9984	-0,32	6,018	0,538	1,248	37	0,973684211	0,072	50	3,927	No	No	_	Hoover 2010
44	124	Narwhal	*Monodon monoceros*	Odontocetes	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	4,062	0,001930783	0,084	26,182	-1,337	3,114	0,052	0,126	8	0,210526316	0,121	77,78	3,927	No	No	_	Hoover 2010
44	125	Bowhead	*Balaena mysticetus*	Mysticetes	Large	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	3,335	0,01086575	0,021	5,4754	-1,998	1,703	0,011	-0,6	2	0,052631579	0,115	66,67	3,927	No	No	_	Hoover 2010
44	126	Walrus N	*Odobenus rosmarus*	Pinnipeds	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	3,332	0,002740255	0,172	47,123	-1,737	2,562	0,021	-0,31	4	0,105263158	0,071	61,11	3,927	No	No	_	Hoover 2010
44	127	Walrus S	*Odobenus rosmarus*	Pinnipeds	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	3,452	0,000986492	0,097	33,778	-0,494	4,248	0,36	1,024	33	0,868421053	0,227	42,59	3,927	No	No	_	Hoover 2010
44	128	Bearded Seal	*Erignathus barbatus*	Pinnipeds	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	3,866	0,003699344	0,176	14,262	-0,751	3,417	0,199	0,664	22	0,578947368	0,165	57,41	3,927	No	No	_	Hoover 2010
44	129	Harbour Seal	*Phoca vitulina*	Pinnipeds	Small	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	3,971	0,001045681	0,125	18,612	-1,539	3,179	0,033	-0,05	6	0,157894737	0,117	72,22	3,927	No	No	_	Hoover 2010
44	130	Ringed Seal	*Pusa hispida*	Pinnipeds	Small	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	4,077	0,04685835	0,158	17,272	-0,0515	3,015	1	1,291	38	1	0,055	61,11	3,927	No	No	_	Hoover 2010
44	131	Harp seal	*Pagophilus groenlandicus*	Pinnipeds	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	4,103	0,001	0,126	15,66	-1,334	3,403	0,052	0,172	11	0,289473684	0,024	57,41	3,927	No	No	_	Hoover 2010
44	132	Beluga E	*Delphinapterus leucas*	Odontocetes	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	3,694	0,002071632	0,066	21,448	-1,631	2,789	0,026	-0,18	5	0,131578947	0,246	72,22	3,927	No	No	_	Hoover 2010
44	133	Beluga W	*Delphinapterus leucas*	Odontocetes	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	3,873	0,02466229	0,064	16,713	-0,294	3,05	0,571	1,068	35	0,921052632	0,222	66,67	3,927	No	No	_	Hoover 2010
44	134	Beluga James	*Delphinapterus leucas*	Odontocetes	Medium	Hudson Bay, Canada	55,668231	-83,631594	ARC	ARCS	1970s	38	40	14	54	3,868	0,001463789	0,087	16,623	-1,318	3,253	0,054	0,159	10	0,263157895	0,202	66,67	3,927	No	No	_	Hoover 2010

N	Ecopath group	Name group	Species aggregation	Group	Relative size	Location	Approximate latitude (Decimal degree)	Approximate longitude (Decimal degree)	Ocean	Ecosystem type	Year	No. of trophic groups (from Keystoneness table)	No. of trophic groups (including Detritus)	No. of fleets	Total No. of groups (from MTI dataset)	TL	B	P/B	Q/B	KS1 Score	KS2 Score	TI	KS3 Score	Ranking (ascending sort KS3)	KS	OI	TD (%)	MTL	Target group	Pedigree	DC Pedigree score	Reference
45	135	Toothed Whales	_	Odontocetes	_	Irish Sea, Ireland,U.K. of Great Britain and Northern Ireland	53,62834	-5,254619	ATL	TEM	1970s	50	53	9	62	4,418	8,00E-05	0,02	8,67	-2,658	3,815	0,002	-0,96	3	0,06	0,276	64,52	3,659	No	No	_	Lees and Makinson 2007
45	136	Baleen Whales	_	Mysticetes	_	Irish Sea, Ireland,U.K. of Great Britain and Northern Ireland	53,62834	-5,254619	ATL	TEM	1970s	50	53	9	62	3,872	0,00034	0,02	10	-0,834	5,011	0,131	0,856	35	0,7	0,299	50	3,659	No	No	_	Lees and Makinson 2007
45	137	Seals	_	Pinnipeds	_	Irish Sea, Ireland,U.K. of Great Britain and Northern Ireland	53,62834	-5,254619	ATL	TEM	1970s	50	53	9	62	4,313	0,011	0,06	14,55	-0,973	3,362	0,095	0,699	27	0,54	0,143	53,23	3,659	No	No	_	Lees and Makinson 2007
46	138	Ceteaceans	*Balaenoptera physalus* , *Balaenoptera acutorostrata* , *Megaptera novaeangliae* , *Physeter catodon* , *Globicephala melaena* , *Balaenoptera borealis* , *Balaenoptera musculus* , *Delphinus delphis* , *Tursiops truncatus* , *Lagenorhynchus acutus*	Odontocetes_Mystyceti	_	Eastern Scotian Shelf, Canada	44,503077	-62,215701	ATL	TEM	1980s	38	39	12	51	3,59	0,2295	0,04	10,17	-0,19	2,838	0,655	1,241	38	1	0,217	62,75	3,545	No	No	_	Bundy 2004
46	139	Grey Seals	*Halichoerus grypus*	Pinnipeds	Medium	Eastern Scotian Shelf, Canada	44,503077	-62,215701	ATL	TEM	1980s	38	39	12	51	4,16	0,025	0,124	11,8	-0,926	3,065	0,12	0,631	20	0,526315789	0,206	62,75	3,545	No	No	_	Bundy 2004
47	140	Dolphins	_	Odontocetes	_	Jurien Bay, Australia	-30,098593	114,835258	IND	TEM	2000s	73	80	14	94	4,047	0,00601927	0,1	41,07	-0,0389	5,272	0,514	1,794	71	0,97260274	1,157	53,19	2,922	No	No	_	Lozano-Montes et al. 2011
47	141	Sea lions	_	Pinnipeds	_	Jurien Bay, Australia	-30,098593	114,835258	IND	TEM	2000s	73	80	14	94	3,925	0,0189	0,099	50,507	-1,084	3,73	0,046	0,715	32	0,438356164	0,519	59,57	2,922	No	No	_	Lozano-Montes et al. 2011
48	142	Baleen Whales	_	Mysticetes	_	Georges Bank, United States of America	41,598467	-69,033102	ATL	TEM	1990s	29	31	1	32	3,699	0,4167178	0,038	4,5	-1,402	1,215	0,033	-0,08	6	0,206896552	0,151	56,25	3,187	No	No	_	Link et al. 2006
48	143	Odontocetes	_	Odontocetes	_	Georges Bank, United States of America	41,598467	-69,033102	ATL	TEM	1990s	29	31	1	32	4,7	0,1127281	0,04	13,83	-0,578	2,606	0,222	0,803	23	0,793103448	0,072	57,25	3,187	No	No	_	Link et al. 2006
49	144	Other mammals	_	_	_	Peru	-11,255004	-78,102901	PAC	UPW	1950s	19	20	1	21	3,364	0,06	0,08	40	-0,985	2,707	0,071	0,191	10	0,526315789	0,109	0,381	2,35	No	No	_	Jarre-Teichmann & Pauly 1993
49	145	Fur seal	*Arctocephalus australis*	Pinnipeds	Small	Peru	-11,255004	-78,102901	PAC	UPW	1950s	19	20	1	21	3,354	0,0001	0,1	31	-3,99	2,48	7E-05	-2,71	2	0,105263158	0,095	0,286	2,35	No	No	_	Jarre-Teichmann & Pauly 1993
49	146	Sea lion	*Otaria flavescens*	Pinnipeds	Medium	Peru	-11,255004	-78,102901	PAC	UPW	1950s	19	20	1	21	3,351	0,0001	0,1	28	-4,09	2,381	6E-05	-2,83	1	0,052631579	0,091	0,238	2,35	No	No	_	Jarre-Teichmann & Pauly 1993
50	147	mammals	_	_	_	Sørfjord, Norway	69,166906	16,769146	ARC	ARCS	1990s	24	25	1	26	4,18	0,01	0,102	35,3	-0,39	3,98	0,45	0,972	22	0,916666667	0,022	53,85	3,29	No	No	_	Falk-Petersen 2004
51	148	Baleen whales	*Balaenoptera edeni* , *Megaptera novaeangliae*	Mysticetes	Large	Lesser Antilles	14,1536	-60,489231	ATL	OCEAN	2000s	30	31	9	40	4,303	0,025127	0,04	12,19	-0,282	3,368	0,388	0,922	27	0,9	0,787	52,5	4,146	Yes	No	_	Mohammed et al. 2008
51	149	Deep-diving whales	*Physeter catodon*	Odontocetes	Large	Lesser Antilles	14,1536	-60,489231	ATL	OCEAN	2000s	30	31	9	40	5,127	0,014536	0,04	5,44	-1,841	2,046	0,011	-0,61	4	0,133333333	1,16	42,5	4,146	Yes	No	_	Mohammed et al. 2008
51	150	Killer whales	*Orcinus orca* , *Orcinus orca* , *Feresa attenuate*	Odontocetes	Large	Lesser Antilles	14,1536	-60,489231	ATL	OCEAN	2000s	30	31	9	40	4,752	0,001582	0,02	9,64	-0,949	3,901	0,083	0,466	13	0,433333333	0,275	55	4,146	Yes	No	_	Mohammed et al. 2008
51	151	Shallow-diving cetaceans	*Globicephala macrorhynchus* , *Peponocephala electra* , *Stenella frontalis* , *Tursiops truncatus* , *Stenella clymene* , *Stenella attenuata* , *Stenella coeruleoalba* , *Lagenodelphis hosei* , *Steno bredanensis*	Odontocetes	_	Lesser Antilles	14,1536	-60,489231	ATL	OCEAN	2000s	30	31	9	40	4,757	0,033621	0,05	13,5	-0,398	3,125	0,297	0,748	23	0,766666667	0,296	42,5	4,146	Yes	No	_	Mohammed et al. 2008
52	152	toothed mammals	*Phocoena phocoena* , *Delphinus delphis* , *Globiecephala melas*	Odontocetes	_	Western Channel, France,U.K. of Great Britain and Northern Ireland	48,8247	-6,799443	ATL	TEM	1970s	50	52	9	61	4,365	0,00576	0,4	13,727	-0,88	3,653	0,101	0,792	32	0,64	0,025	52,46	2,782	No	No	_	Araújo et al. 2005
52	153	seals	*Haliochoerus grypus* , *Phoca vitulina*	Pinnipeds	_	Western Channel, France,U.K. of Great Britain and Northern Ireland	48,8247	-6,799443	ATL	TEM	1970s	50	52	9	61	4,629	0,003	0,04	13,32	-0,311	4,505	0,374	1,379	48	0,96	0,18	46,77	2,782	No	No	_	Araújo et al. 2005
53	154	Bottlenose dolphin	*Tursiops truncatus*	Odontocetes	Medium	Cyprus insular shelf trophic model	34,704165	33,559838	MED	TEM	2015	38	40	5	45	4,291	0,024868	0,084	11,01	-0,413	0	0,385	1	3	0,078947368	0,528	53,33	3,254	No	No	_	Michailidis et al. 2019
53	155	Monk seal	*Monachus monachus*	Pinnipeds	Medium	Cyprus insular shelf trophic model	34,704165	33,559838	MED	TEM	2015	38	40	5	45	4,288	0,002	0,126	11,66	-0,457	4	0,348	1	4	0,105263158	0,193	55,56	3,254	No	No	_	Michailidis et al. 2019
54	156	Dolphins	*Tursiops truncatus*	Odontocetes	Medium	Gulf of Gabes	34,42365	11,949022	MED	TEM	2000	39	41	6	47	4,339	0,079745	0,075	14	-0,431	2,476	0,29	1,061	5	0,128205128	0,099	0,468	3,439	No	No	_	Hattab et al. 2013
55	157	dolphins	*Delphinus delphis* , *Phocoena phocoena* , *Stenella coeruleoalba* , *Tursiops truncatus*	Odontocetes	_	North Aegean (Greece,Turkey)	40,781551	25,235349	MED	TEM	2003	38	40	5	45	4,579	0,01	0,083	13,808	-1,209	2	0	0,048	1	0,026315789	0,127	55,56	3,474	No	No	_	Tsagarakis et al.2010

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Supplementary Material 2 for the article: The role of mammals as key predators in marine ecosystems

DATA EXPLORATION AND MODELS VALIDATION

Consumption/biomass ratio (QB) as a function of body size

We classified 85 marine mammal species into three different body size classes (see Table S2). We compiled information about the average weight of 85 species, of which 81 species comprised species from the 55 Ecopath models. We made our classification based on the available information about marine mammals' specific average weights from the literature (Table S2). We assumed that the sex ratios were the same in all marine mammal populations used. We used the first and third quartiles taken from all average weight estimates to classify functional groups, 115 kg and 1202.5 kg (see Table S2), respectively, and divided the mammal groups into three class sizes: small (< 115 kg), medium-sized (>115.1 kg and < 1202.5 kg), and large marine mammals (> 1202.5 kg). We used only adult weights to obtain the quartiles. Information about the species aggregations of functional groups was taken from published food web models (see Supplementary Material—SM1). Functional groups including different body size species were not included in this classification. Subsequently, we modelled consumption/biomass ratio (QB) as a function of body size, adding ecosystem type—open ocean, Arctic shelf, temperate coastal and shelf areas, and tropical coastal and shelf areas—as a random effect in a gamma linear mixed model, with a log link function. We found that QB decrease with increasing body size (Figure S1); individual classified as 'larger' body size, has lower the QB (Medium Body Size Estimate = 0.725; $z = 0.160$; $p < 0.01$; Small Body Size Estimate = 0.975; $z = 0.212$; $p < 0.01$).

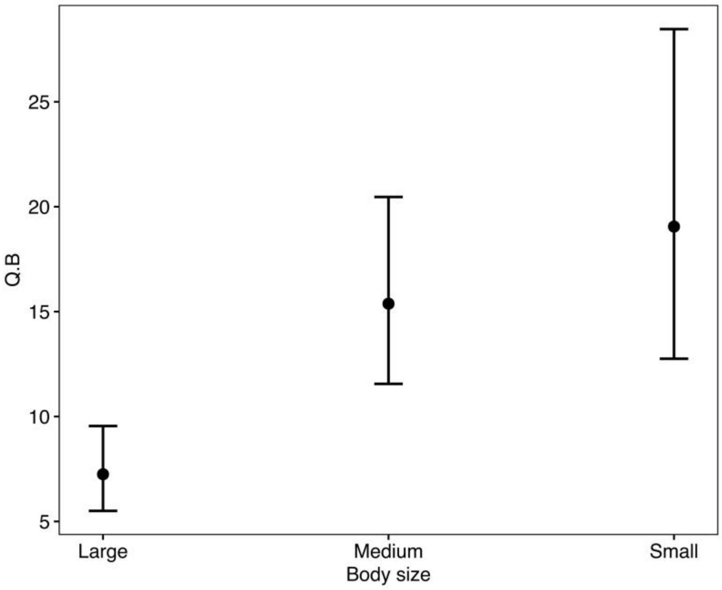

Figure S1. Predict effect of body size on consumption/biomass ratio (QB); Points are predicted values. Bars represent the 95% confidence interval of predicted values.

Trophic levels by Clades

We found that Mysticetes use lower trophic level when compared with the other two clades (Figure S2). This variation across clades in terms of trophic level or even in terms of the effect of the explanatory variables on TI and KS motivated us to include clade as additive or interactive covariate in our linear models (see main text).

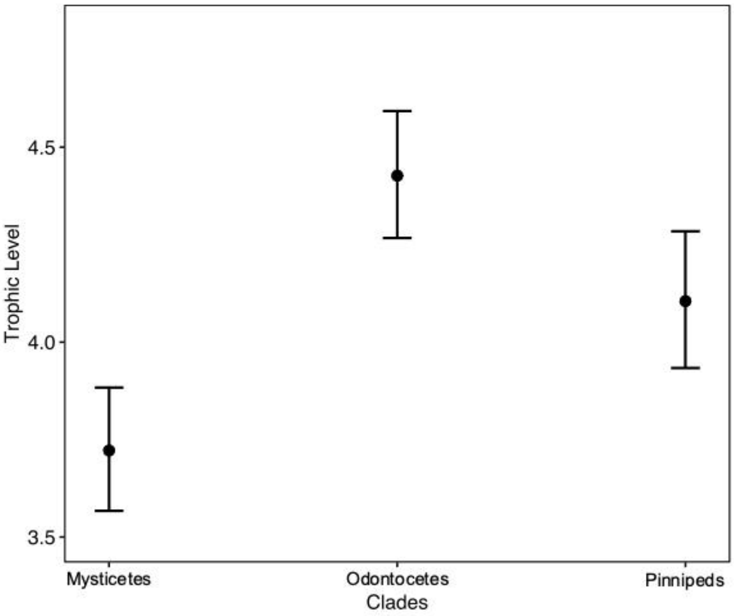

Figure S2. Predict effect of Clade on trophic level (*TL*); Points are predicted values. Bars represent the 95% confidence interval of predicted values.

Models validation

We validated the most parsimonious models for trophic impact (*TI*) and keystoneness index (*KS*) using the package DHARMa, in R (see methods in main text), which simulate 10000 datasets from the fitted model and tested if deviations between the observed (see methods in main text) and expected residuals distribution were significant. Plots below show the validation results. Figure S3a shows results for model that fits *TI* as a function of *TL* and Biomass interacting with clades, and S3b shows results for model that fits *KS* as a function of *TL* and Biomass interacting with clades. Both QQ-plots did not detect overall deviations from the expected distribution, and the dispersion test, the *KS* test and the outlier test are not significant. The residual versus predicted plots also did not show any pattern, suggesting no violation of the model assumption.

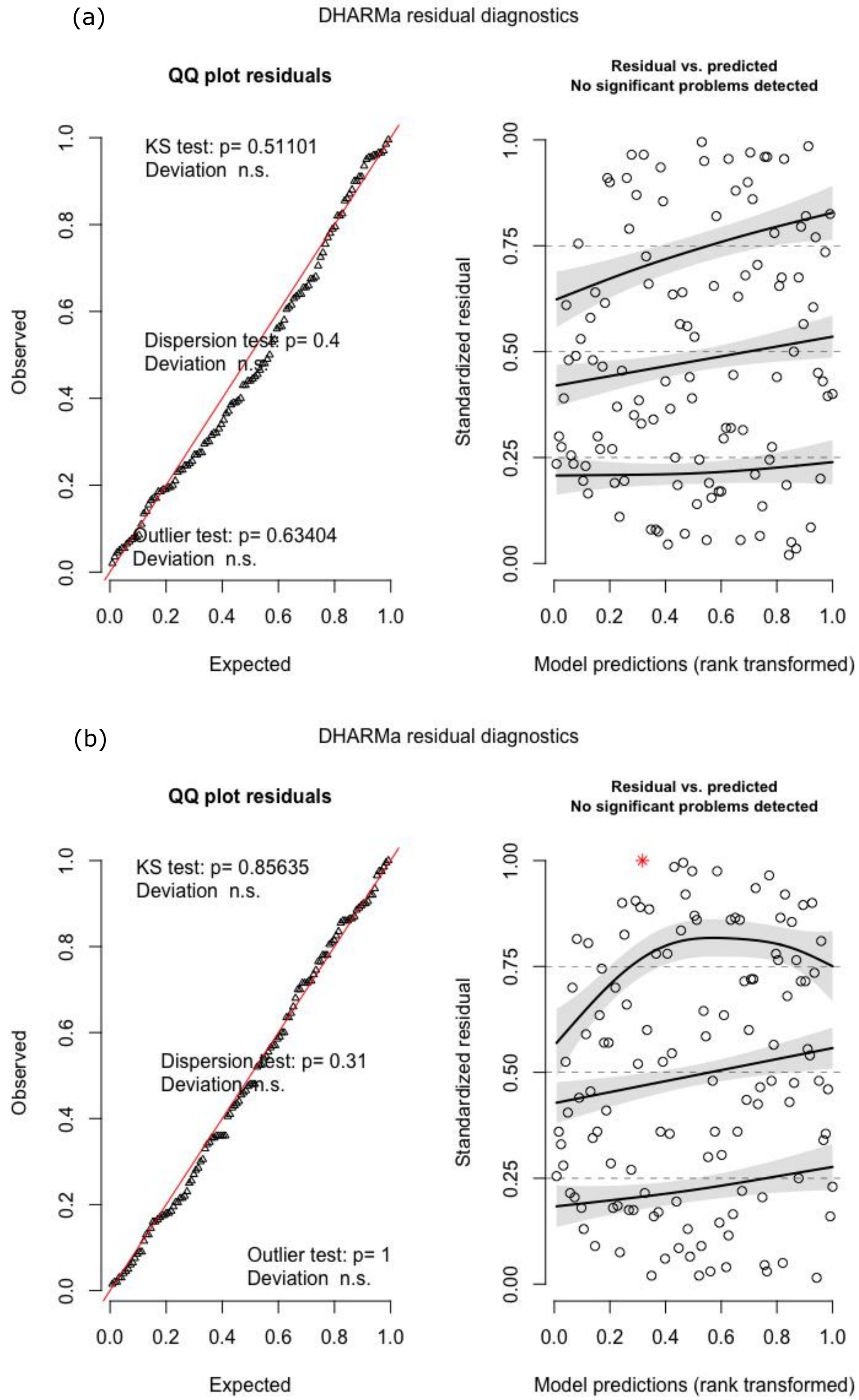

Figure S3. Testing model assumption by simulating residuals. (a) shows QQ-plot and residual versus predicted plots for trophic impact most parsimonious model, whereas (b) shows QQ-plot and residual versus predicted plots for keystoneness index most parsimonious model.

GLOSSARY

Direct Trophic Effect: when predation pressure of a certain predator affects the density of its prey (Yodzis 2001).

Food Intake: the product of the biomass of a living group (B) multiplied by its consumption/biomass ratio (QB), expressed as a ratio (e.g., t · km^{-2} · year-1) (Christensen et al. 2008).

Functional Group: compartment in a food web that includes several species that have similar ecological and feeding characteristics, or even species in the same taxonomic group (Christensen et al. 2008).

Indirect Trophic Effect: when the increase of predation pressure by a predator on a prey species affects the density of a third species without contact (Yodzis 2001).

Keystone Species: species with relatively low abundance (or rather relatively low biomass) with a structuring role in the food web (Libralato et al. 2006, Heithaus et al. 2008).

Trophic Impact (Total): a mass-balanced-model outcome based on Leontief input-output network analysis, which considers all pathways of all lengths in a food web and expresses the relative change of biomass in all compartments, resulting from an infinitesimal biomass gain of the assessed compartment (Leontief 1951, Hannon 1973, Ulanowicz & Puccia 1990).

Table S2. Classification of 85 marine mammal species into three different body size classes.

	Average weight (kg)			Source	Body size class
Species	**Newborns**	**Male**	**Female**		
Arctocephalus australis	4	140	50	Bastida & Rodríguez 2003	Small
Arctocephalus gazella	5.5	170	40	Bastida & Rodríguez 2003	Small
Arctocephalus pusillus pusillus	5-12	279	76	Jefferson et al. 2011	Medium
Phocoena dioptrica	?	110	100	Bastida & Rodríguez 2003	Small
Balaena mysticetus	?	70,000 - 90,000?		Reeves & Leatherwood 1985	Large
Balaenoptera acutorostrata	?	20,000 - 27,000		Stewart & Leatherwood 1985	Large
Balaenoptera borealis	680	20,000	22,000	Bastida & Rodríguez 2003	Large
Balaenoptera brydei Olsen, 1913 and/or B. edeni Anderson, 1879	700	15,500 - 16,600		Bastida & Rodríguez 2003	Large
Balaenoptera musculus	2,500	115,000	125,000	Bastida & Rodríguez 2003	Large
Balaenoptera physalus	2,000	50,000	55,000	Bastida & Rodríguez 2003	Large
Berardius arnuxii	?	6,500?		Bastida & Rodríguez 2003	Large
Callorhinus ursinus	5.4-6	270	50	Jefferson et al. 2011	Medium
Caperea marginata	?	30,000	35000	Bastida & Rodríguez 2003	Large
Cephalorhynchus commersonii	6	40	42	Bastida & Rodríguez 2003	Small

Cystophora cristata	20-30	192-352	145-300	Jefferson et al. 2011	Medium
Delphinapterus leucas	80-100	423.75	408.57	Sergeant & Brodie 1969	Medium
Delphinus delphis	?	110	90	Bastida & Rodríguez 2003	Small
Enhydra lutris	2.04 - 2.27	27 - 38.6	16 - 27	Kenyon 1981	Small
Erignathus barbatus	33.6	215		Burns 1981	Medium
Eschrichtius robustus	920	?	35,000	Jefferson et al. 2011	Large
Eubalaena australis	2,000	40,000	45,000-60,000	Bastida & Rodríguez 2003	Large
Eubalaena glacialis/Eubalaena japonica*	?	?	90,000	Jefferson et al. 2011	Large
Eumetopias jubatus	18-22	1,000	273	Jefferson et al. 2011	Medium
Feresa attenuata	10	170	160	Bastida & Rodríguez 2003	Medium
Globicephala macrorhynchus	?	3,000?		Bernard & Reilly 1999	Large
Globicephala melas	75	2,200	1,300	Bastida & Rodríguez 2003	Large
Grampus griseus	20-30	380		Bastida & Rodríguez 2003	Medium
Halichoerus grypus	11-20	170-310	105-186	Bastida & Rodríguez 2003	Medium
Histriophoca fasciata	10,5	90	148	Jefferson et al. 2011	Medium
Hydrurga leptonyx	30	350	450	Bastida & Rodríguez 2003	Medium
Hyperoodon ampullatus	?	7,500-10,000		Fernández et al. 2014	Large
Hyperoodon planifrons	?	6,000-7,500		Bastida & Rodríguez 2003	Large
Inia geoffrensis	?	150	90.13	Best & da Silva 1989	Medium

Kogia breviceps	25	300		Bastida & Rodríguez 2003	Medium
Kogia simus	35	240		Bastida & Rodríguez 2003	Medium
Lagenodelphis hosei	20	180?	160?	Bastida & Rodríguez 2003	Medium
Lagenorhynchus acutus	?	235?	182	Jefferson et al. 2011	Medium
Lagenorhynchus albirostris	40	180-150		Jefferson et al. 2011	Medium
Lagenorhynchus australis	20?	100	90	Bastida & Rodríguez 2003	Small
Lagenorhynchus cruciger	?	80	77	Bastida & Rodríguez 2003	Small
Lagenorhynchus obliquidens	?	200	150	Reeves & Leatherwood 1985	Medium
Lagenorhynchus obscurus	6	80	70	Bastida & Rodríguez 2003	Small
Leptonychotes weddelli	25	380	400	Bastida & Rodríguez 2003	Medium
Lissodelphis peronii	12	100	90	Bastida & Rodríguez 2003	Small
Lobodon carcinophagus	20	200	220	Bastida & Rodríguez 2003	Medium-
Megaptera novaeangliae	650	30,000	35,000	Bastida & Rodríguez 2003	Large
Mesoplodon bidens	?	1,000-1,300		Reeves & Leatherwood 1985	Medium
Mesoplodon densirostris	60	800	1,000	The Society for Marine Mammology 2019	Medium-
Mesoplodon europaeus	?	1200?		Reeves & Leatherwood 1985	Medium
Mesoplodon grayi	?	1000		Bastida & Rodríguez 2003	Medium-

Mesoplodon hectori	?	500?		The Society for Marine Mammology 2019	Medium
Mesoplodon layardii	?	1,200		Bastida & Rodríguez 2003	Medium
Mesoplodon mirus	?	1,020	1,400	Reeves & Leatherwood 1985	Large
Mesoplodon spp.	?	565	791	Mead 1989	Medium
Mirounga leonina	40	4,000	800	Bastida & Rodríguez 2003	Large
Monachus monachus		320	300	The Society for Marine Mammology 2019	Medium
Monodon monoceros	80	769.6	504.4	Hay & Mansfield 1989	Medium
Odobenus rosmarus	63.3 - 63.8	1,215.1	811.5	Fay 1981	Medium
Ommatophoca rossii	17	173	180	Bastida & Rodríguez 2003	Medium
Orcinus orca	190	7,500	4,500	Bastida & Rodríguez 2003	Large
Otaria flavescens	13	300	150	Bastida & Rodríguez 2003	Medium
Pagophilus groenlandicus (=*Phoca groenlandica*)	10	130	120	Jefferson et al. 2011	Medium
Peponocephala electra	15	210		Reeves & Leatherwood 1985	Medium
Phoca vitulina	8 - 12	70 - 150	60 - 110	Jefferson et al. 2011	Small
Phoca hispida (=*Pusa hispida*)	4 - 5	50 - 70		Jefferson et al. 2011	Small
Phoca largha	7 - 12	82 - 123		Jefferson et al. 2011	Small

Phocoena sinus	7.5	45 - 50		Reeves & Leatherwood 1985	Small
Phocoena phocoena	4 - 5	45 - 70		Reeves & Leatherwood 1985	Small
Phocoenoides dalli	11	170 - 200	180	Reeves & Leatherwood 1985	Medium
Physeter macrocephalus	1,000	40,000	20,000	Bastida & Rodríguez 2003	Large
Pontoporia blainvillei	7	35	45	Bastida & Rodríguez 2003	Small
Pseudorca crassidens	80	2,250	1,000	Bastida & Rodríguez 2003	Large
Sotalia guianensis	?	85.9		Emygdio Leite de Araujo Monteiro Filho 2018. Personal communication.	Small
Sousa teuszii	14	~142.2	~123.2	Reeves & Leatherwood 1985	Medium
Stenella attenuata	10	100	90	Bastida & Rodríguez 2003	Small
Stenella clymene	?	45 - 79		Perrin & Mead 1994	Small
Stenella frontalis	?	94.7		Perrin et al. 1994	Small
Stenella coeruleoalba	12	150	130	Bastida & Rodríguez 2003	Medium-
Stenella longirostris	?	66 - 75	55 - 65	Perrin & Gilpatrick Jr. 1994	Small
Steno bredanensis	?	90 - 155		Miyazaki & Perrin 1994	Medium
Tursiops truncatus	20	300	280	Jefferson et al. 2011	Medium
Ursus maritimus	0.6	800	350 - 500	Jefferson et al. 2011	Medium

Zalophus californianus	6 - 6.7	392.5	110.6	Odell 1981	Medium
Zalophus wollebaeki	25	250?	50 - 100	Jefferson et al. 2011	Medium
Ziphius cavirostris	260	2,500		Bastida & Rodríguez 2003	Large

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CAPÍTULO 2: To be or not to be controlled? The ecological role of the Guiana-dolphin in its southernmost range

Abstract: Several studies have explored dolphins feeding ecology in coastal ecosystems, however, gauging the predatory effects of dolphins on ecosystem, which may be applied to management and conservation effort, lacks of further investigations still. Along the northwestern section of the Bay of Santa Catarina Island, locally known as North Bay, in Southern Brazil, inhabits the southernmost population of the Guiana-dolphin (*Sotalia guianensis*). This small and resident population is structured in a large and highly cohesive group, using a small home range restricted to the western section of the bay. Like many other coastal dolphins, this dolphin population negatively interact with fisheries, with frequent bycatch events or by sharing feeding resources. To explore the ecological role of dolphins in the North Bay ecosystem, we constructed an Ecopath food web model to estimate ecosystem and compartmental attributes. Mixed Trophic Impact and Keystoness index were used to assess the importance of the species in the ecosystem. Complementarily to the Ecopath approach, we used Ecological Network Analysis (ENA) to assess the ecological role of the compartments using Control Analysis and the Throughflow centrality. According to our model, North Bay is a mature Detritus-based ecosystem. As expected, dolphins showed the highest keystoneness score value among all functional groups, while Control Analysis showed they are also the most controlled component in the ecosystem. Then, we conclude that the Guiana-dolphin inhabiting the North Bay is a crucial compartment in the ecosystem, as it shows the greatest ecosystem impact per biomass among all compartments, whilst it is the most vulnerable compartment. Finally, we conclude that the dolphins rely mostly on Micropogonias furnieri, the latter being the main food web hub showing the greatest centrality of flows.

Keywords: *Sotalia guianensis* · Delphinidae · Odontoceti · Brazil · food web · ecological function · Ecopath · Ecological Network Analysis · *Micropogonias furnieri* .

INTRODUCTION

The species' ecological function refers to how the species can influence other species in their communities and ecosystems (Estes 2009). It is widely accepted as a general pattern that marine mammals play a crucial role in many aquatic ecosystems (Katona & Whitehead 1988).

Cetaceans, specifically, are believed to play an essential role in their ecosystem because of properties such as large body size, high metabolic rates, feeding ecology, trophic position, high abundance, behaviourally mediated indirect interactions, and capability for large-scale movements (Bowen 1997, Pauly et al. 1998, Kiszka et al. 2015).

However, the ecological role of many marine mammal species and the likely cascading effects of and on mammals in marine ecosystems are still to be unveiled (Bowen 1997, Kiszka et al. 2015, Estes et al. 2016). To study how mammals affect marine ecosystems, we may take two main general approaches. The first is quasi-experimental studies evaluating the ecosystem changes in the food web outcoming from the non-purposeful removal of the subject drivers being assessed, which is logistically challenging and time-consuming (Englund & Cooper 2003). The second is by using ecological modeling, which provides a holistic way and framework to probe the ecological role of species in aquatic ecosystems (Ulanowicz & Puccia 1990).

The Guiana-dolphin (*Sotalia guianensis* van Benédén, 1864) is a small-bodied delphinid that inhabits coastal and shallow waters, frequently found in inshore environments such as estuaries and bays (da Silva et al. 2010, Flores et al. 2018). This species typically occurs associated with runoffs and may occasionally be found upstream to the limit of tidally influenced waters (da Silva and Best 1996). It is distributed continuously along the Atlantic Coast of Central (Honduras, 15°58'N) and South America (South of Brazil, 27°35'; da Silva and Best 1996, Simões-Lopes, 1988).

In North Bay, Southern Brazil, inhabits a small resident populationof 123 ± 35 Guiana-dolphin individuals (Ditt-Pfundstein et al. 2014) in the southernmost limit of distribution for the species (Simões-Lopes 1988, Wedekin et al. 2007). This population motivated the establishment, in 1992, of the Anhatomirim Environmental Protected Area, which has the primary aim of protecting these dolphins. Within this protected area, some fishing operations such as gill nets are restricted, while surrounding this area, and throughout the North Bay, the environment sustains several fisheries that can negatively interact with these dolphins via bycatch events or by competing for feeding resources (Simões-Lopes & Ximenez 1990, Ferreira et al. 2006, Medeiros et al. 2006).

Over the last decade, several studies have explored the diet and feeding ecology of the Guiana-dolphins using stomach content analysis (Cremer et al. 2012, Lopes et al. 2012, Rodrígues et al. 2020). These studies revealed that the Guiana-dolphins deploy characteristic feeding plasticity across their range, suggesting opportunistic and generalist foraging habits, which shows its capability to feed on a large spectrum of prey occurring in different climatic conditions (Rupil et al. 2018). Both demersal and pelagic fish species have been reported as main prey for Guiana-dolphins (Daura-Jorge et al. 2011) and a recent isotope-based study confirmed the high trophic level and coastal-dependent diet of the Guiana-dolphins in North Bay (Teixeira et al. 2021). However, the ecological role of the Guiana-dolphin has not been explored from a food web perspective yet.

As a two-step fashion, we aimed first to describe the North Bay ecosystem structure and functioning, and so then we stressed the Guiana-dolphin's ecological role through a food web model (Ecopath approach) and Ecological Network Analysis (ENA) to unveil its influence on the food web. We hypothesized that the Guiana-dolphin displays an essential function as keystone species in the North Bay ecosystem, given that the species is a small-sized homeothermic predator showing characteristic trophic plasticity and feeding on a higher trophic level. We then discuss the implications of our findings in terms of coastal ecosystems management and the conservation of small coastal dolphins' populations.

MATERIALS & METHODS

STUDY AREA

North Bay, in Southern Brazil (27° 30' S and 48° 35' W; Fig. 1), is the northern section of the Bay of Santa Catarina Island. It is surrounded by heterogeneous shores, with a continuum of rocky shores, sand beaches, and mangroves. The North Bay's oceanographic parameters are similar to adjacent external waters, and the ecosystem dynamics are mostly influenced by tidal currents and freshwater runoffs (Simonassi et al. 2010). The bay's surface area is about 200 km^2, with an average depth of 5 m and a maximum, 21 m. The water temperature in the bay varies widely according to seasonal changes (15 – 29° C), and the average sea surface temperature is 22.5° C (Simonassi et al. 2010).

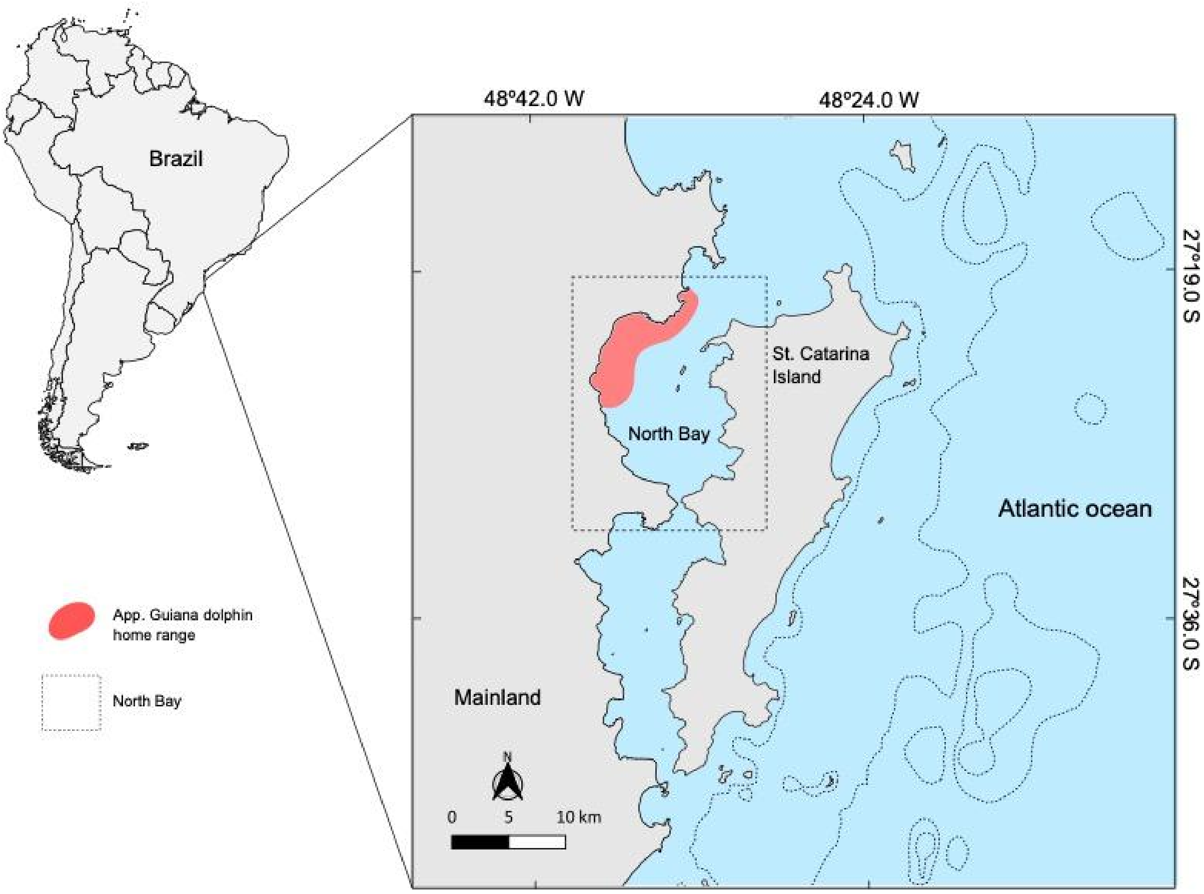

Figure 1. Study area. In the North Bay of Santa Catarina island (27° 30’ S and 48° 35’ W), Southern Brazil, inhabits a resident population of about 123 individuals, which is the southernmost population of the Guiana-dolphin (*Sotalia guianensis*).

ECOPATH MODEL APPROACH

Ecopath is a modeling framework based on the ecosystem approach originally proposed by Polovina (1984), which has been under continuous development of modules and methods since then (Christensen & Pauly 1992, Christensen & Walters 2004, Christensen et al. 2008). Parameterization for Ecopath models is based on the steady-state principle, which assumes all functional groups/species are mass-balanced. Ecosystem models can be constructed with Ecopath based on inter-specific feeding relationship ranges through a defined trophic network. The most straightforward mass-balance Ecopath master equation for each functional group (i) can be expressed as:

$$Bi*PBi = \sum Bj*QBj*DCji + Yi + BAi + NMi + Bi*PBi*(1-E \tag{1}$$

where: Bi is Biomass of prey i, PBi is the production-biomass ratio (PB) of i, Bj is the Biomass value of predator j, QBj is the consumption-biomass ratio of predator j, DCji is the diet composition or proportion of prey i in the diet of predator j, Yi is the total fishery catch of i, BA is the biomass accumulation rate for i, NM is the net migration rate (emigration—immigration) of i, and EE is the ecotrophic efficiency or non-predation natural mortality of i. An Ecopath mass-balance model provides a ‘snapshot’ quantified by the flows throughout the food web. Ecopath can compute many ecosystems and ecological attributes, including, in our case, the trophic impact of a group on other species and a set of keystoneness indices (Christensen & Pauly 1992; see also http://www.ecopath.org).

NORTH BAY MODEL: DESCRIPTION AND PARAMETERIZATION

The topology of the North Bay food web model comprises 21 compartments, of which 20 groups are organisms (Dolphins, Seabirds, 11 fish compartments, Turtles, Shrimp, Crabs, Squids, Benthos, Zooplankton, and Primary producers) and one group of Detritus. The majority of compartments are grouping different species which has the same feeding habits and ecological characteristics like the habitat use along the water column (Table SM1).

VERTEBRATES: DOLPHINS AND SEABIRDS

Given that the Guiana-dolphin population is the object of this study, we gave special attention to the parameterization of this compartment. According to the most recent estimation available (Ditt-Pfundstein et al. 2014), the Guiana-dolphin’s total population size in North Bay is 123 individuals (CI 95% = 92 – 163). Given that we did not know the age structure of the dolphin population and given that we only had sufficient data to estimate the adults’ average weight (which may bias the biomass estimation), we assumed the minimum value (92), and we considered all adults with 85.9 kg by an individual as average weight (Emygdio

Leite de Araújo Monteiro Filho, personal communication). The total biomass (7.9 t) was divided by the approximate total area (200 km^2) to obtain the biomass parameter value (B = 0.039 t * km^{-2}). The production to biomass (PB) parameter value was obtained using the mortality rate estimation (Allen 1971). To estimate the survival for the Guiana-dolphin in the North Bay, we took the weighted average out of four estimations from previous studies: 0.88 ± 0.07 /year (Cantor et al. 2012); 0.90 ± 0.02 /year (Schulze, personal communication); 0.86 ± 0.066 /year (Mello et al. 2019); and 0.85 ± 0.05 /year (Souza 2013); which estimate was 0.868 /year.

Given that the mortality rate is equal to 1 minus the survival rate, the PB rate was assumed to be 0.132 * year^{-1}. This observed mortality rate is quite similar to 0.1, which is the input PB value previously used in a former study that estimated such parameter based on the longevity of marine mammals (Hoenig 1983, Trites et al. 1997). To obtain the consumption rate value (QB), we compared two approaches, which were the indirect estimate of food requirement based on specific body size (Trites et al. 1997) and direct estimations from a study on a related species (Kastelein et al. 1999). The Guiana-dolphin diet in the North Bay of Santa Catarina was described through stomach content analysis and was described estimating the Index of Relative Importance (IRI) of all identified prey (Daura-Jorge et al. 2011).

Other species of mammals co-exist with the Guiana-dolphins in the North Bay. Otters (*Lontra longicaudis*) are a resident species using permanently and year-round the North Bay habitats, while bottle-nose-dolphins (*Tursiops truncatus*) are transient users. However, given the lack of reliable information about abundance estimates, we did not consider these species in our food web model.

Unfortunately, no accurate estimation of the Seabirds was made in North Bay. Thus, biomass was estimated by Ecopath using a low (and common for seabirds) EE value (0.001). The PB and QB values were taken from a model made for a tropical bay in Brazil (Angelini et al. 2018). The diet of birds was based mainly on general knowledge and information available from a previous study (Branco et al. 2005). Further detail about the construction of the North Bay food web model can be found in the Supplementary Material (SM) attached to this current chapter of the thesis.

FISH

The fish biomass parameter estimations were based on Cattani et al. (2016), who described the fish assemblage of the North Bay in 2005, using seasonal samplings with bottom trawls carried out in six pre-established areas. Trawls net had 4 cm at the mouth, a width of 8.65 m, and a height of 1.80 meters (15.57 m^2 opening). Further detail about the fish sampling can be found in Daura-Jorge (2007). Information about the species' trophic guilds was taken from Elliott et al. (2007) and the classification used by Barletta and Blaber (2007).

We obtained the fish PB and QB ratios parameter values through indirect estimates using empirical relationships. We took the Pauly (1980) equation for Natural Mortality (M) to calculate the PB for fish compartments, and for consumption, we used the empirical regression of Palomares and Pauly (1998). Parameters values for these estimates were obtained from the FishBase platform (Froese and Pauly, 2017). All specific PB and QB parameter values were weighted within the groups according to the species relative contributions to the biomass of each group defined (Christensen et al., 2005). Further information about the equations used to estimate PB and QB parameters can be found in the SM attached to this Chapter.

BENTHOS

The composition of the benthic community and its biomass was described by Pagliosa (2005), which used 36 sampling sites uniformly distributed along the North Bay in 2001. Information to estimate vital parameters is from Netto et al. (2018). The benthic community's PB parameter value was estimated indirectly using Thomas Brey's conversion (Brey 2001). The QB parameter value was taken from another tropical and coastal model (Angelini et al. 2018).

ZOOPLANKTON

The stock of zooplankton was sampled in three sites along the North Bay from May 2014 through April 2017 as part of the routine sampling program of ASF lab. Plankton samples were collected in surface horizontal hauls with a 200 µm cylindrical - conical net, with 0.5 m in diameter, equipped with a flowmeter. The PB and QB ratio values for the zooplankton group were taken from another tropical and coastal model (Angelini et al. 2018).

PRIMARY PRODUCERS

We used Chlorophyll *a* values as proxy of phytoplankton biomass to estimate the primary producers' standing crop for our North Bay food web model. We used remote sensing using the MODIS Chlorophyll a layer (https://worldview.earthdata.nasa.gov/), which provides the near-surface concentration of chlorophyll *a* in milligrams of chlorophyll pigment per cubic meter (mg*m^{-3}) in the ocean. We took the average concentration of Chlorophyll *a* from 01st January 2014 through 31th December 2015 (7.618 ± 4.105 mg * m^{-3}). Please see SM for further detail about how Chlorophyll *a* can be estimated using data from MODIS.

We converted Chlorophyll *a* data to wet weight as Angelini et al. (Angelini et al. 2018), assuming the euphotic zone is about 3 m deep (Leonardo Rörig, pers. comm., 2020) and obtained a range value between 6.85 g * m^{-2} and 7.65 g * m^{-2}. The primary productivity was also taken from the Araça Bay food web model (Angelini et al. 2018), which was considered a similar ecosystem in terms of climate conditions.

FISHERY LANDINGS

We used information on artisanal fishery landings provided by the "Projeto de Monitoramento da Atividade Pesqueira no Estado de Santa Catarina –PMAP-SC" (available in pmap-sc.acad.univali.br). We analyzed the artisanal catch landings reported from August 2016 through July 2017 in the Biguaçú municipality. The yearly total catch estimated for the system was 106.6 tons. The catch was comprised mainly on shrimp, whitemouth croaker (*Micropogonias furnieri*), catfish, and largehead hairtail (*Trichiurus lepturus*).

BALANCING OF THE FOOD MODEL AND VALIDATION

We used the unassimilated consumption rate of Benthos and Zooplankton unto 40% (Heymans et al. 2016) but maintained other compartments with 20% (details in Supplementary Material). We increased some biomass values of fish groups underestimated initially during data sampling to find EE values lower than one since EE was used as the verification criteria to balance the food web model (Kavanagh et al. 2004). We estimated the index of quality of input data (Pedigree index), and found an overall pedigree value of 0.451, categorized as being high (Morissette 2007). The validation of a static model as the Ecopath is estimated with the calculation of the Pre-balance analysis (Prebal), which estimates the relation among Trophic Level and the parameters B, PB and QB (Link 2010; Heymans et al. 2016). These relations should be negative. We also estimated some rates as: Respiration/Assimilation, Respiration/Biomass and Production/Consumption for each compartment (Link 2010, Heymans et al. 2016; please see Figure SM2 and SM3 in the SM attached to this Thesis for details).

NETWORK ANALYSIS

SYSTEM LEVEL ASSESSMENT

The Ecopath framework provides a set of general indicators to characterize the ecosystem as a whole (Christensen et al., 2008), in terms of flows rather than biomass (Ulanowicz 1986), and it can be quantified using the Total System Throughput (TST). The TST is the sum of all transfers of all compartments throughout the system (Christensen 1995, Patrício et al. 2004). The maturity and stability of the system were quantified in two complementary measures, namely: ascendancy and overhead. Ascendancy (A) is an abstract concept that combines ecosystem size and trophic organization (Ulanowicz 1980). Otherwise, all the imports, exports, as well as respirations contribute to the measurement of overhead, and it measures the inefficiencies of throughputs. In other words, the overhead represents the cost to the system to operate the way it does, but it also represents the degree of freedom and the capability of the system to reconfigure itself after a disturbance (Baird et al. 1991). We used the “Lindeman spine” to aggregate the energy flow networks into their canonical forms (Ulanowicz 1997). Among the connectance indices, we used the Finn Cycling Index (FCI), which reveals the proportion of TST that is recycled in the system (Patrício et al. 2004), and it can be used as a measure of stress. The higher the FCI, the greater the proportion of TST recycled, even though cycling seems to be a measure of stress rather than maturity (Odum 1969, Baird et al. 1991).

COMPARTMENTAL ASSESSMENT

The predatory effects of compartments in the North Bay food web was quantified using the Relative Trophic Impact (*TI*) and the keystoneness index (*KS#3*) to joining the interaction strength (Ulanowicz & Puccia 1990) and the critical role (Valls et al. 2015) of functional groups, respectively. Complementarily to the indicators available in Ecopath, we use the Ecological Network Analysis (ENA) approach, which is a mathematical methodology to study the interactions between components of a system structure (connectance pattern), function (flow regime), and boundary inputs (Higashi & Burns 1991). Particularly, we explored the ecological role of dolphins using the enaControl function in enaR (Borrett & Lau, 2014, Scharler & Fath 2009). Control analysis quantifies the relative influence of one node (i.e., compartment) exerts on another through the network flows and it also can be used to assess the ecological role of each component in the system (Bentley et al. 2019).

A network is defined as a system of compartments and connections (Fath et al. 2019). Thus an Ecopath food web model can be considered as a network of nodes and arcs and then proceed to the conversion to a network object suitable to apply ENA in 'enaR' (Borrett and Lau, 2014). To convert our Ecopath model into a network object, we extracted the ENA model information from Ecopath (Borrett, personal communication) as follows: (1) Internal flows from the Ecopath consumption matrix, (2) Imports for heterotrophs were identified on the Ecopath basic inputs, while for primary producers the import is the net primary production, (3) network exports was extracted directly from the Ecopath inputs, (4) respiration from Ecopath outputs, (5) node storage from Ecopath biomass, and (6) a logical vector indicating whether the nodes are living or not. The respiration of primary producers was assumed to be 10% of the net primary production (Brown et al. 1991, Erikson 1998, Robinson & Williams 2005, Williams & Lefevre 2008). Data were input as $t * km^{-2} * year^{-1}$.

We used the system control (sc_j), which is computed from the Control difference (CD) matrix to quantify the overall system's control (Schramski 2006, 2007). The cd_{ij} values of the CD matrix are the respective differences of the fractional transfer values ($n_{ij} - n_{ji}$) between two components, H_i and H_j. In an open-loop control system, if a component H_i contributes more energy-matter to H_j than H_j to H_i, then H_i controls H_j (Schramski 2006). Thus, sc_j values, which are obtained by the summation of all cd_{ij} ($cd_{.j} = sc_j$), gauge the relative influence of each functional group regarding the energy fractional transfer through the system and measures the role of each component by quantifying pairwise dependencies (Schramski et al. 2006, 2007).

The control difference enables system-based comparisons across the entire matrix and the direction of control is denoted by + or - (Schramski et al. 2006, 2007). A positive sc_j value indicates the group has a controlling influence over the system, while a negative sc_j indicates that the group is controlled by the system. The summation of cd_{ij} and sc_{ij} are equal to zero, denoting total system balance (Schramski et al. 2006, 2007). We additionally measured the trophic overlap among dolphins and other compartments, including the trophic overlap between dolphins and fisheries (Morisita estimate) using the *spaa* package in R (Zhang 2016).

We finally took the throughflow centrality as a global indicator of compartmental functional importance (Borrett 2013). Throughflow centrality is the total energy or matter entering or exiting a system component (Borrett 2013) and is defined as the sum of all flows in or out of a given component in the system (Fath et al. 2019).

RESULTS

SYSTEM LEVEL INDICATORS FROM ECOPATH MODEL

The balanced model for North Bay ecosystem has Dolphin, Seabirds, Demersal Piscivorous and Squids as the main top-predators (Table 1). The fish total biomass is 5.36 t * km^{-2} including the main Dolphin's prey, Pelagic planktivorous and *M. furnieri* (see Diet Composition in Table SM4). The Pre-balance analysis and rates estimates showed the model is biological and physiologically accurate (see Supplementary Material), as high trophic level groups showed lower PB and QB rates.

As to the information indexes, total system throughput (TST) equal to 13366.09 t * km^{-2} * year^{-1}, ascendency (25.51%), and specific overhead (ϕ/TST) with 74.49% show a high system redundancy. Besides, three connectance indices, the overall connectance (0.212), the system omnivory (0.156) and the Finn cycling index with 39.14% of total throughput, display a system high cycling. The path of flows through the North Bay food web is summarized in Figure 2, elucidating that the detritus pathway is four times higher than primary productivity.

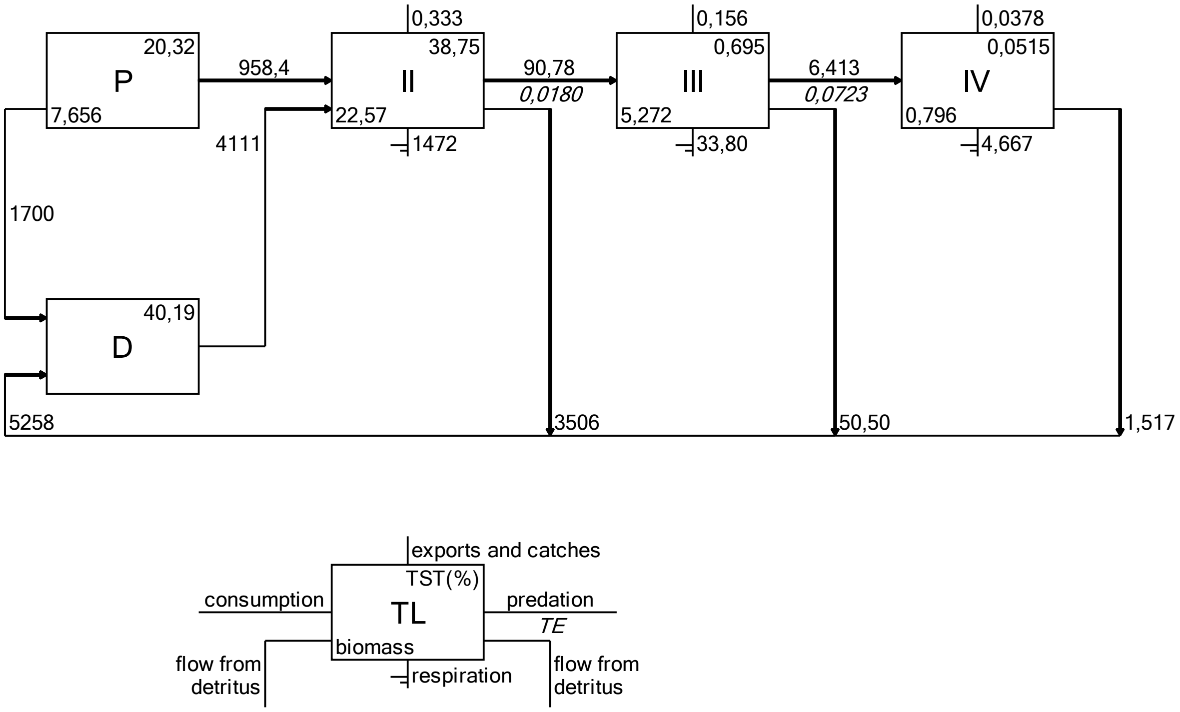

Figure 2. The Lindeman spine showing the energy-matter flux chain of the North Bay ecosystem (Brazil) aggregated into their canonical forms. Abbreviations are as follow: D, Detritus; P, Primary producer; TL, trophic level (II, III, and IV); TE, trophic efficiency; TST(%), Fraction of Total System Throughput expressed as percent. Flows units are expressed as t * km^{-2} * year^{-1}.

Table 1. Basic estimates of the North Bay balanced Ecopath model.P/B: Production/Biomas; Q/B: Consumption/Biomass; EE: Ecotrophic Efficiency; P/Q: Production/Consumption. Bold values were estimated by Ecopath model.

FUNCTIONAL GROUP	Trophic level	Biomass (t/km^2)	P/B (/year)	Q/B (/year)	EE	Landing (t/km^2/year)
Dolphin	**4.08**	0.039	0.132	14.6	**0**	-
Seabird	**4.07**	**0.001**	0.4	50	0.001	-
Benthopelagic opportunist	**3.58**	0.31	1.23	9.54	**0.99**	-
Demersal opportunist	**2.75**	1	0.98	8.05	**0.78**	-
Demersal piscivorous	**3.95**	0.3	1	11.19	**0.96**	-
Demersal zoobenthogagous	**3.05**	1.3	1.95	4.78	**0.97**	-
Catfish	**3.05**	1.258	0.81	2.45	**0.3**	0.03
Micropogonias furnieri	**3.1**	0.5	1.08	5.73	**0.87**	0.11
Mugil spp.	**2**	1	0.45	12.21	**0.53**	-
Trichiurus lepturus	**3.83**	0.3	0.39	3.33	**0.97**	0.05
Pelagic piscivorous	**3.74**	0.012	0.48	4.59	**0.96**	-
Pelagic planktivorous	**2.77**	1.4	2.14	11.76	**0.99**	-
Pelagic miscellaneous	**2.96**	0.3	3.13	11.48	**0.78**	-
Turtle	**2.05**	0.003	0.15	2.54	**0**	-
Shrimp	**2**	0.059	7.75	26.7	**0.723**	0.33
Crab	**2.84**	0.027	1.4	19.08	**0**	-
Squids	**3.81**	0.073	2.26	14.22	**0.78**	-
Benthos	**2.05**	11.209	125.79	354	**0.11**	-
Zooplankton	**2.1**	8.8	40	160	**0.6**	-
Primary producers	**1**	7.656	347.17	-	**0.36**	-
Detritus	-	-	-	-	**0.92**	-

THE DOLPHIN TROPHIC ROLE

The mixed trophic impacts (MTI) analysis revealed direct and indirect trophic interactions among compartments in the North Bay of Santa Catarina food web model (Fig. 3). The Dolphins group has a higher negative impact on its main prey *M. furnieri*, *T. lepturus*, and Pelagic planktivorous. Dolphins also has a soft positive and indirect impacts on Benthos and Demersal miscellaneous/opportunists. Also, as it can be seen by means of the MTI, increasing both the primary productivity and detritus stock would potentially enhance the biomass of Benthos, which in turn is the main prey for *M. furnieri,* thus benefitting the Dolphins. Benthos exerts the highest overall impact on food web, however, the keystone index (KS#3) indicates the Guiana-dolphin is the main key species in the North Bay food web model (Table 2) followed, respectively, by Benthopelagic miscellaneous/opportunist and Zooplankton (Table 2).

COMPARTMENTAL ASSESSMENT FROM ENA APPROACH

The system control (SC) of each functional group can be defined as either positive (> zero) or negative (< zero). The majority of components, including Dolphins, have SC values below zero, indicating that they are controlled by other components in the network, while Dolphin showed the lowest SC value that means that the species is the one group most controlled by the system (Table 2). Turtle, Pelagic piscivorous, and Seabird have SC values above zero, indicating that they control other components.

Additionally, Dolphins has some of the largest niche overlap estimates along other compartments. In descending order are: Dolphin with Seabird (0.767), Dolphin with *Trichiurus lepturus* (0.485), with Cephalopod (0.477), with Benthopelagic miscellaneous/opportunist (0.345), with Pelagic miscellaneous/opportunist (0.273), and with Demersal piscivorous (0.25). Furthermore, the Morisita trophic overlap measure between the dolphins and the fishery was rather low (0.232).

Finally, *Micropogonias furnieri* showed the highest throughflow centrality estimate, indicating that it is globally the most dominant node (i.e., the hub component) in the system (see Table 2).

Table 2. Keystone index #3 (KS#3), Relative Total Impact TI, System Control (SC_j), and Throughflow centrality (T_j) for the North Bay Ecopath food web model compartments (ordered in KS#3 descending value). The KS#3 and TI are outcomes from the Ecopath model, while the SC_j and T_j are outcomes from the ENA approach. For ease of interpretation, values are sorted in KS#3 scores descending order. Highlighted in bold the highest T value.

Functional group	**TI**	**KS#3**	**SC_j**	**T_j**
Dolphins	0.208	1.201	-28.57	0.119
Benthopelagic opportunist	0.239	1.058	-18.02	0.974
Zooplankton	0.86	0.915	-3.67	915.2
Demersal piscivorous	0.123	0.885	-26.86	0.973
Trichiurus lepturus	0.103	0.77	-26.09	0.261
Squids	0.077	0.712	-18.39	0.459
Micropogonias furnieri	0.112	0.682	-7.87	**1000364**
Benthos	1	0.679	-3.55	2997.281
Pelagic opportunist	0.071	0.572	-7.01	1.627
Primary producers	0.243	0.542	-0.002	5316.271
Pelagic planktivorous	0.125	0.474	-6.41	6.289
Shrimp	0.041	0.467	-7.19	0.445
Demersal opportunist	0.064	0.39	-10.26	2.588
Demersal zoobenthophagous	0.083	0.379	-5.29	3.777
Seabirds	0.01	-0.017	160.29	0.008
Catfish	0.024	-0.093	-6.63	1.6
Mugil spp.	0.029	-0.251	-10.4	5.21
Pelagic piscivorous	0.0051	-0.354	27.48	0.017
Crabs	0.003	-0.655	-9.62	0.142
Turtles	0	-3.7	11.28	0.002
Detritus	-	-	-3.12	4111.003

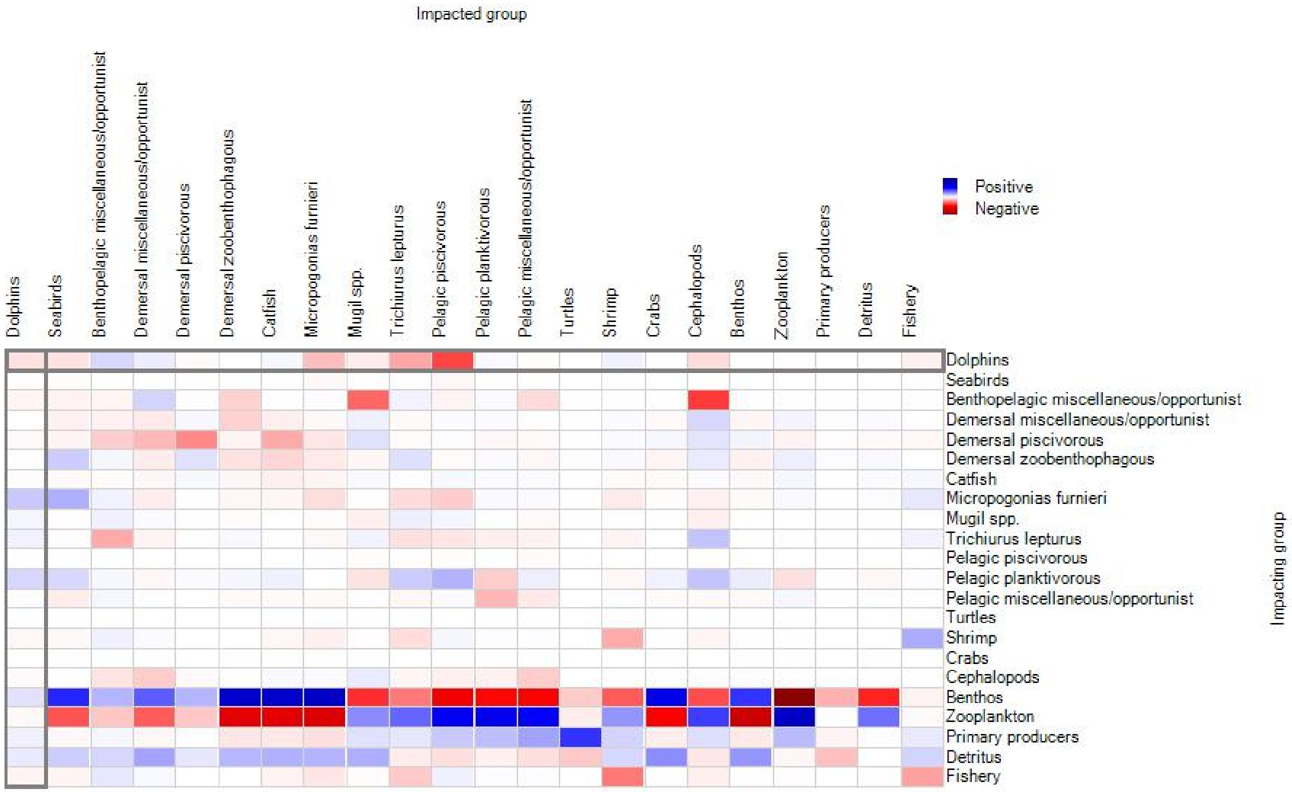

Figure 3. Mixed Trophic Impacts (MTI) analysis of the North Bay ecosystem. Negative (red) and positive (blue) impacts are represented. Trophic Impact (TI) is defined as the percentage of a compartment's activity that could affect and is being affected by, either positively or negatively, any other compartment (both in direct and indirect ways through the food web). TI values range between 0 and 1, with values close to 1 indicating higher trophic impact. The grading of colors indicate the interaction strength from higher positive impact TI values (dark blue) to higher negative impact TI values (dark red).

DISCUSSION

Our main results show that the North Bay food web is based primarily on Detritus. Therefore, North Bay can be characterized as being a mature, detritus-based, and thus a likely resilient ecosystem (Fath et al., 2019). Furthermore, the Guiana-dolphin is a key species in the North Bay with the highest trophic level and high trophic overlap with other species. Dolphins have a marked impact on *M. furnieri*, Pelagic piscivorous, and *T. lepturus*. However, Dolphins exert beneficial effects upon some of their own prey given indirect effects. Otherwise, ENA approach considers Dolphins as the most vulnerable node to removing other controlling nodes and that *M. furnieri* is hub species in the North Bay food web.

We identified some cases of mutually beneficial trophic interactions among Guiana-dolphins and their prey and competitors by direct or indirect trophic interactions. There are four fish groups showing positive trophic impact values even though they are Dolphins' prey (Table SM 5): Benthopelagic miscellaneous, Demersal miscellaneous, Demersal zoobenthophagous, and Pelagic planktivorous. The positive trophic impact values of these groups show that the direct detrimental effect of predation by the dolphins is overshadowed by the indirect beneficial trophic effects of the dolphins' predation upon potential predators and/or competitors of their prey. The beneficial effects of the predation of marine mammals on other components of food webs by indirect interactions and cascading effects have also been reported in previous studies (Abrams et al. 1996, Yodzis 2001, Gregr et al. 2020). Thus, given the complexity of trophic interactions, the predatory role of the Guiana-dolphin in the North Bay may have penetrating effects throughout the food web, and that such effects can benefit even the dolphins' prey.

We highlight that the two approaches that we took here—Mixed Trophic Impact (MTI) and Ecological Network Analysis (ENA; Control Difference, CD)—must be interpreted differently, while they can be used as complementary methods in order to assess ecological role. Interestingly, although the MTI matrix is not strictly antisymmetric (Ulanowicz & Puccia 1990), the CD matrix is, indeed, antisymmetric (Schramski 2006). Such difference between these two matrices' configurations appears to happen because the MTI accounts for competition since it considers both the direct and indirect effects of interactions (Lima et al. 2020), as it considers all pathways of all lengths in a food web (Ulanowicz & Puccia 1990). In other words, while the MTI is the system-wide effect—either positive or negative—of each component on other components, resulting from an infinitesimal change in the biomass of components as derived from a specific food web connectance pattern (Ulanowicz & Puccia

1990), control analysis (CD) focuses on the dominance relationships or dependence of components from each other in terms of the directions of energy-matter delivery throughout the food web (Schramski et al. 2007).

Controllability relates to the vulnerability of components (Siljak 1991). If structural changes alter the connections and the removal of connections destroys input reachability (Siljak 1991), nodes might be especially affected by removing controllers. In other words, the more controlled a species is, the higher might be its vulnerability to the impact resulting from the removal of controlling species. Thus, we can conclude that special attention must be given to the dolphins because they are the most controlled compartment in the North Bay ecosystem. It seems a contradiction: the main key species (estimated by Ecopath) is also the most controlled species (estimated by ENA). The answer for this contradiction is that while MTI assesses the effects of changes in the biomass of components, it lacks information in terms of the effect of its removal (Allesina & Boldini 2004), which is computed by controllability evaluation. Thus, we can conclude that, although the biomass variation of dolphins has penetrating effects throughout the food web as we showed by the MTI and keystoneness index, the dolphins depend strongly on other donor compartments for their energy-matter storage, because it is a top-predator. According to previous reports, we should expect a certain tendency of energy flows to donor-oriented control of lower trophic levels on higher trophic levels (Fath 2004, Bentley et al. 2019). However, this was not the case for Seabirds in our model, maybe because the Ecopath estimated the Seabirds biomass in a low value. Thus, the Seabirds' energy demands in the North Bay food web model are low also.

We also explored the pairwise relationship between the fishery and dolphins, and we concluded that, although the trophic overlap observed between them was rather low, these two compartments may compete with each other for some food resources, such as for *M. furnieri*. Regarding the overall pairwise effect between Dolphins and Fishery, direct effects (predation) dominate over indirect effects (competition) for both compartments, so that the overall trophic interaction is detrimental for one another. Although the catch in the North Bay targets mainly shrimp, *M. furnieri* is also an important fish prey caught by the fishery (PMAP-SC). Furthermore, *M. furnieri* is the most important prey for both the dolphins and some of the most abundant seabirds in the North Bay (Daura-Jorge et al. 2011, Branco et al. 2005). Thus, *M. furnieri* should be the species that weighs most in the coefficient of variation of interactions among the higher trophic level compartments in the North Bay food webs, such as dolphins and the fishery. Finally, we identified *Micropogonias furnieri* as the species showing the greatest throughflow centrality value. Thus, as the throughflow centrality is considered a global indicator of node importance, which means that it includes the direct and indirect exchanges among all the compartments (Borrett 2013), we conclude *M. furnieri* is the most important hub in the North Bay food web.

Finally, it is foremost to emphasize that there are seminal evidence showing that the identification of keystone species, although in many cases challenging chore, is of critical importance for the maintenance of ecosystems, since their removal can cause profound shifts, including changes in species' richness, biomass, biodiversity, and community structure (Power et al. 1996). Furthermore, ecosystem-based management actions should focus on species' functionality rather than rarity (Jordán 2009). Therefore, protecting a key species such as the Guiana-dolphins is important for the food web as a whole and special attention should be given to the conservation of dolphin populations.

Our Ecopath model and ENA approach are limited, especially because of the data set. The most appropriate calibration method for an Ecopath model is to fit it to a time series (biomass or catch) of the main species (Serpetti et al. 2017, Bortnatowski et al. 2018). Unfortunately, we have no temporal monitoring for our functional groups. However, our approaches are trusting because the physiological rates seem tangible. A time series for the main species (Dolphin, *M. furnieri* – catch and biomass) and for Seabirds could improve the model's confidence and, consequently, the management actions.

CONCLUSION

We can conclude that the Guiana-dolphin is a keystone species in the North Bay ecosystem. The dolphins show major impact on the food web due to both direct and indirect effects. Also, although the North Bay can be considered as a resilient system, the control of the system on Guiana-dolphins might make the species likely vulnerable to biotic and abiotic structural changes, such as the removal of controllers. Furthermore, *Micropogonias furnieri* is the most important hub in the North Bay food web model in terms of its contribution to the total throughflows (including fishing activities). Thus, the importance of managing *M. furnieri* goes beyond the fact that this fish species is a main food resource for the dolphin as well as a target catch for the fishery, but rather due to its overall importance for the food web. Additionally, we believe that the combined use of the keystoneness indices and ENA approach can facilitate the adoption of management measures by decision makers (Fath et al. 2019). Therefore, our results should be taken into account in both the formulation of ecosystem management policies in the North Bay and conservation efforts to protect the Southernmost population of the Guiana-dolphin.

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Supplementary Material

To be or not to be controlled? The ecological role of the Guiana-dolphin in its southernmost habitat in the world

Table SM1. Information on each functional group in the North Bay food web model and the data sources for parameters for each species and functional group.

	Functional group name	**Species aggregation**	**B**	**P/B**	**Q/B**	**Diet**	**Catch**
1	Dolphins	*Sotalia guianensis*	Ditt-Pfundstein et al. 2014	Cantor et al. 2012, Schulze 2021, de Mello et al. 2019, Souza, 2013	Trites et al. 1997, Kastelein et al. 1999	Daura-Jorge et al. 2011	
2	Seabirds	*Fregata magnificens*, *Sula leucogaster*	Ecopath estimate	Angelini et al. 2018	Angelini et al. 2018	Branco et al. 2005	
3	Benthopelagic opportunist	*Chloroscombrus chrysurus*, *Selene setapinnis*, *Trachinotus carolinus*, *Peprilus paru*	Daura-Jorge 2005	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese and Pauly 2017	Froese & Pauly 2017	
4	Demersal opportunist	*Chaetodipterus faber*, *Eucinostomus argenteus*, *Orthopristis ruber*, *Haemulopsis corvinaeformis*, *Gymnothorax ocellatus*, *Ophichthus gomesii*, *Ctenosciaena gracilicirrhus*, *Menticirrhus americanus*, *Odontoscion dentex*, *Diplectrum radiale*, *Archosargus rhomboidalis*, *Prionotus punctatus*, *Etropus crossotus*	Daura-Jorge 2005	Indirect estimate: Froese and Pauly 2017	Indirect estimate: Froese and Pauly 2017	Froese & Pauly 2017	

	Functional group name	Species aggregation	B	P/B	Q/B	Diet	Catch
5	Demersal piscivorous	*Achirus declivis*, *Porichthys porosissimus*, *Centropomus parallelus*, *Centropomus undecimalis*, *Citharichthys spilopterus*, *Cynoscion jamaicensis*, *Cynoscion leiarchus*, *Cynoscion microlepidotus*, *Isopisthus parvipinnis*, *Macrodon ancylodon*, *Synodus foetens*	Daura-Jorge 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese & Pauly 2017	Froese & Pauly 2017	
6	Demersal zoobenthophagous	*Achirus lineatus*, *Trinectes paulistanus*, *Selene vomer*, *Symphurus tesselatus*, *Diapterus rhombeus*, *Eucinostomus gula*, *Eucinostomus melanopterus*, *Stephanolepis hispidus*, *Zapteryx brevirostris*, *Paralonchurus brasiliensis*, *Micropogonias furnieri*, *Stellifer brasiliensis*, *Stellifer rastrifer*, *Umbrina* sp., *Sphoeroides spengleri*, *Sphoeroides testudineus*, *Sphoeroides tyleri*	Daura-Jorge 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese and Pauly 2017	Froese & Pauly 2017	
7	Catfish	*Genidens barba*, *Genidens genidens*	Daura-Jorge 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese & Pauly 2017	Froese & Pauly 2017	PMAP-SC (Biguaçú)
8	*Micropogonias furnieri*	*Micropogonias furnieri*	Daura-Jorge 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese and Pauly 2017	Froese & Pauly 2017	PMAP-SC (Biguaçú)
9	*Mugil* spp.	*Mugil curema*, *Mugil platanus*	Daura-Jorge 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese & Pauly 2017	Froese & Pauly 2017	
10	*Trichiurus lepturus*	*Trichiurus lepturus*	Daura-Jorge 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese & Pauly 2017	Froese & Pauly 2017	PMAP-SC (Biguaçú)

	Functional group name	Species aggregation	B	P/B	Q/B	Diet	Catch
11	Pelagic piscivorous	*Anchoa spinifera*, *Lagocephalus laevigatus*	Daura-Jorge 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese & Pauly 2017	Froese & Pauly 2017	
12	Pelagic planktivorous	*Harengula clupeola*, *Opisthonema oglinum*, *Platanichthys platana*, *Anchovia clupeoides*, *Cetengraulis edentulus*	Daura-Jorge 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese & Pauly 2017	Froese & Pauly 2017	
13	Pelagic opportunist	*Oligoplites saurus*, *Pellona harroweri*	Daura-Jorge, 2007	Indirect estimate: Froese & Pauly 2017	Indirect estimate: Froese & Pauly 2017	Froese & Pauly 2017	
14	Turtles	*Chelonia mydas*	Guesstimate	Angelini et al. 2018	Angelini et al. 2018	Seminoff et al. 2002	
15	Shrimp	*Farfantepenaeus paulensis*, *Farfantepenaeus brasiliensis*, *Litopenaeus schmiti*, *Xiphopenaeus kroyeri*, *Rimapenaeus constrictus*, *Sicyonia typica*, *Sicyonia dorsalis*, *Macrobrachium carcinus*	Freire, pers. comm. 2017	Angelini et al. 2018	Angelini et al. 2018	Branco & Moritz Jr. 2001	PMAP-SC (Biguaçú)
16	Crabs	*Callinectes danae*, *Callinectes ornatus*, *Portunus spinimanus*, *Persephona crinita*, *Eucratopsis crassimanus*, *Hepatus pundibundus*, *Petrolisthes armatus*, *Pyromaia tubercullata*	Freire, pers. comm. 2017	Angelini et al. 2018	Angelini et al. 2018	Medina Mantelatto & Petracco 1997, Mantelatto & Christofoletti 2001	
17	Squids	*Lollingucula brevis*	Freire, pers. comm. 2017	Coll et al., 2013	Coll et al. 2013	Coll et al. 2013	
18	Benthos	Polychaeta (Ampharetidae, Amphinomidae, Arabellidae, Capitelidae, Cirratulidae, Cossuridae, Flabelligeridae,	Pagliosa , Pers. comm. 2019	Indirect estimate: used the Thomas	Angelini et al. 2018	Word 1979	

	Functional group name	Species aggregation	B	P/B	Q/B	Diet	Catch
		Glyceridae, Goniadidae, Hesionidae, Lumbrineridae, Magelonidae, Maldanidae, Nephtyidae, Nereididae, Onuphidae, Opheliidae, Orbiniidae, Owenidae, Paraonidae, Pectinaridae, Pholoididae, Phyllodocidae, Pilargidae, Poecilochaetidae, Polynoida, Polyodontidaee, Sabellidae, Sigalionidae, Spionidae Syllida, Terebellidaee, Trichobranchidae), Oligochaeta, Mollusca (Bivalve, Gastropoda), Crustacea (Amphipoda, Cumacea, Leptostraca, Decapoda, Isopoda, Ostracoda, Tanaidacea), Echinodermata (Ofiuroidea), Cephalochordata (Anphioxus), Echiura, Foraminifera, Nematoda, Nemerta, Sipuncula, Platyhelminthes (Turbelaria), Anthozoa, Phoronida		Brey's conversion spreadsheets (Brey 2001)			
19	Zooplankton	Amphipoda, Apendicularia, Bivalve, Brachyura, Caprelideo, Caridea, Chaetognata, Cirripedia cipris, Cirripedia nauplius, Cladocera, Cnidaria, Copepoda, Ctenophoro, Foraminifera, hydrozoans, Isopoda, larvae of Cypris, larva of carideo, larva of Gastropoda, larva of invertebrate, larva of Sipuncula, larva of Phoronida, larvacea, larvae of Bivalvia, larvae of Decapoda, larvae of Echinodermata, larvae of fish, larvae of Polychaeta, Lucifer faxoni, Luciferidae, Megalopa de Brachyura, nauplius (unidentified), nauplios of Cirripedia, Nematoda, Ostracoda, egg of fish (elliptical), egg of fish (rounded), egg of fish, Porcellanidae, Protozoan (Decapoda), Protozoans, Salpa, Siphonophorae, Stomatopoda, Urochordata, zoea of Brachyura, zoea of Caridea	Freire, pers. comm., 2017	Angelini et al. 2018	Angelini et al. 2018	Angelini et al. 2018	
20	Primary Producers	-	https://worldview.earthdata.nasa.gov/	Angelini et al. 2018			
21	Detritus	-	Ecopath estimate				

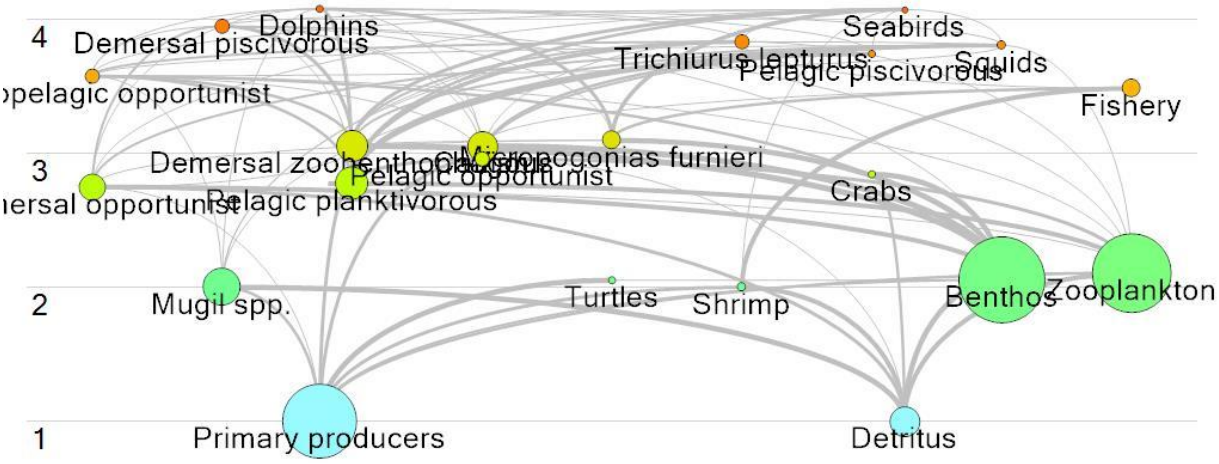

Fig. SM1. Topology and flow regime of the 21 trophic groups of the North Bay food web model plus the fishery along a trophic level gradient.

Pedigree Index

Table SM2. Pedigree index values to evaluate the data quality of Ecopath model for North Bay (Brazil). B: Biomass, P/B: Production/Biomass, Q/B: Consumption/Biomass; DC: Diet Composition (1 = best quality, 0 = poor quality).

	Group name	**B**	**P/B**	**Q/B**	**DC**	**Catches**
1	Dolphins	1	1	0.6	1	
2	Seabirds	0.7	0.2	0.2	0.7	
3	Benthopelagic opportunist	0.7	0.5	0.5	0.2	
4	Demersal opportunist	0.7	0.5	0.5	0.2	
5	Demersal piscivorous	0.7	0.5	0.5	0.2	
6	Demersal zoobenthophagous	0.7	0.5	0.5	0.2	
7	Catfish	0.7	0.5	0.5	0.2	0.7
8	*Micropogonias furnieri*	0.7	0.5	0.5	0.2	0.7
9	Mugil spp.	0.7	0.5	0.5	0.2	
10	*Trichiurus lepturus*	0.7	0.5	0.5	0.2	0.7
11	Pelagic piscivorous	0.7	0.5	0.5	0.2	
12	Pelagic planktivorous	0.7	0.5	0.5	0.2	
13	Pelagic opportunist	0.7	0.5	0.5	0.2	
14	Turtles	0	0.2	0.2	0.2	
15	Shrimp	0.7	0.2	0.2	0.2	0.7
16	Crabs	0.7	0.2	0.2	0.7	
17	Squids	0.7	0.2	0.2	0.7	
18	Benthos	0.7	0.5	0.2		
19	Zooplankton	0.7	0.2	0.2		
20	Primary producers	0.4	0.2			
21	Detritus	0				

Table SM3. Diet composition matrix.

	Prey\Predator	1	2	3	4	5	6	7	8	9	10
1	Dolphins										
2	Seabirds										
3	Benthopelagic opportunist	0.0004	0.0025			0.05					0.15
4	Demersal opportunist	0.008	0.0048			0.15			0.025		
5	Demersal piscivorous	0.0314	0.0525			0.08					
6	Demersal zoobenthophagous	0.0203	0.2875	0.2	0.05	0.31			0.025		0.15
7	Catfish					0.08					
8	*Micropogonias furnieri*	0.2999	0.4249			0.05					
9	*Mugil* spp.	0.0466	0.0041	0.1							0.1
10	*Trichiurus lepturus*	0.1	0.0077								
11	Pelagic piscivorous	0.0096	0.0065								
12	Pelagic planktivorous	0.1885	0.2004	0.2		0.05					0.42
13	Pelagic opportunist	0.086		0.1		0.025					0.1
14	Turtles										
15	Shrimp		0.0008								
16	Crabs										
17	Squids	0.0092	0.0076	0.05							0.005
18	Benthos			0.25	0,6	0.025	1	1	0.95		
19	Zooplankton			0.1	0.01	0.08					0.075
20	Primary Producers				0.04					0.2	
21	Detritus				0.3					0.8	
	Import	0.2	0.001			0.1					
	Sum	1	1	1	1	1	1	1	1	1	1

	Prey\Predator	11	12	13	14	15	16	17	18	19
1	Dolphins									
2	Seabirds									
3	Benthopelagic opportunist							0.05		
4	Demersal opportunist							0.145		
5	Demersal piscivorous									
6	Demersal zoobenthophagous							0.15		
7	Catfish									
8	*Micropogonias furnieri*									
9	*Mugil* spp.	0.1								
10	*Trichiurus lepturus*									
11	Pelagic piscivorous									
12	Pelagic planktivorous	0.65		0.333				0.4		
13	Pelagic opportunist	0.25						0.145		
14	Turtles									
15	Shrimp									
16	Crabs									
17	Squids									
18	Benthos				0.05		0.8			0.1
19	Zooplankton		0.7	0.333				0.11	0.05	
20	Primary Producers		0.3	0.3	0.95	0.3			0.15	0.25
21	Detritus			0.034		0.7	0.2		0.8	0.65
	Import									
	Sum	1	1	1	1	1	1	1	1	1

Table SM4. Mixed Trophic Impact matrix.

	Impacting\Impacted	1	2	3	4	5	6	7	8	9	10	11
1	Dolphins	-0.133	-0.126	0.176	0.0767	-0.0238	0.000750	0.0331	-0.284	-0.0770	-0.386	-0.817
2	Seabirds	-0.00922	-0.0138	0.000015	0.00574	-0.00406	-0.00234	0.00451	-0.0287	-0.000141	0.00249	-0.0361
3	Benthopelagic opportunist	-0.0432	-0.0550	-0.0428	0.193	0.00761	-0.202	-0.00996	0.0111	-0.666	0.0538	-0.0512
4	Demersal opportunist	0.00134	-0.0593	-0.0630	-0.0899	0.0369	-0.199	-0.0723	-0.0309	0.0650	-0.0207	0.0197
5	Demersal piscivorous	-0.0257	-0.0465	-0.218	-0.315	-0.521	-0.0546	-0.376	-0.114	0.134	-0.0162	0.0120
6	Demersal zoobenthophagous	0.00592	0.222	0.0399	-0.0819	0.132	-0.127	-0.179	-0.0954	-0.0332	0.140	-0.0163
7	Catfish	-0.00774	-0.0250	-0.0176	-0.0372	0.0321	-0.0356	-0.0647	-0.0484	0.0276	-0.00403	0.0291
8	*Micropogonias furnieri*	0.241	0.352	0.0629	-0.0790	0.00260	-0.0379	-0.0347	-0.150	-0.00921	-0.157	-0.226
9	*Mugil* spp.	0.0422	-0.00896	0.0658	0.0164	-0.00229	-0.0181	0.000066	-0.0165	-0.0683	0.0731	0.0436
10	*Trichiurus lepturus*	0.0627	-0.0127	-0.371	-0.0510	-0.0144	0.0290	0.00522	-0.0324	0.0526	-0.135	-0.112
11	Pelagic piscivorous	0.00531	0.00474	-0.000424	0.00104	-0.000452	0.000251	-0.000079	-0.00230	-0.0115	-0.00672	-0.0131
12	Pelagic planktivorous	0.177	0.173	0.0370	-0.0355	0.0180	0.0380	0.0676	0.000867	-0.123	0.229	0.335
13	Pelagic opportunist	0.00657	-0.0797	0.0384	-0.00250	0.000183	-0.0249	-0.0214	-0.0200	-0.0105	-0.0410	0.0155
14	Turtles	-0.000001	-0.000002	-0.000001	-0.000001	-0.000001	-0.000003	-0.000003	-0.000003	0.000001	0.000001	0.000001
15	Shrimp	-0.0337	-0.0286	0.0644	0.0183	0.00112	-0.000509	-0.0359	-0.0704	-0.0102	-0.147	0.0405
16	Crabs	-0.000337	-0.00250	-0.000857	-0.00187	-0.000858	-0.00422	-0.00422	-0.00440	0.00240	0.00153	0.00327
17	Squids	-0.0194	0.000966	-0.116	-0.229	-0.0234	0.00506	0.0278	0.0165	0.0881	-0.0407	-0.0679
18	Benthos	0.127	0.952	0.325	0.708	0.326	1.606	1.608	1.674	-0.919	-0.584	-1.248
19	Zooplankton	-0.0291	-0.751	-0.250	-0.718	-0.247	-1.377	-1.373	-1.437	0.509	0.678	1.206
20	Primary Producers	0.0653	-0.0297	0.0388	-0.00596	-0.111	-0.102	-0.140	0.135	0.108	0.241	0.288
21	Detritus	0.193	0.225	0.178	0.398	0.110	0.313	0.346	0.332	0.353	-0.0789	-0.144
22	Fishery	-0.0538	-0.0469	0.103	0.0294	0.00185	-0.000764	-0.0574	-0.113	-0.0161	-0.235	0.0650

	Impacting\Impacted	12	13	14	15	16	17	18	19	20	21	22
1	Dolphins	0.0259	-0.0137	-0.000152	0.0593	0.00386	-0.154	0.00538	-0.00741	-0.000444	-0.00224	-0.0610
2	Seabirds	-0.00235	0.000975	-0.000088	0.00322	0.000348	-0.00201	0.000505	-0.000509	-0.000119	-0.000281	-0.00354
3	Benthopelagic opportunist	0.0196	-0.164	0.00279	-0.00230	-0.00128	-0.863	-0.00253	0.00428	0.00307	0.00375	0.00585
4	Demersal opportunist	0.0168	0.00388	0.00460	0.0177	-0.0278	0.171	-0.0396	0.0461	0.00693	0.0195	-0.00195
5	Demersal piscivorous	-0.0331	-0.0262	-0.00637	0.0174	0.0334	0.117	0.0479	-0.0568	-0.00923	-0.0248	-0.0375
6	Demersal zoobenthophagous	0.0185	-0.0382	0.00764	0.0256	-0.0428	0.0888	-0.0612	0.0732	0.0113	0.0312	-0.000426
7	Catfish	0.0195	0.0204	0.00402	-0.0196	-0.0228	0.0202	-0.0326	0.0383	0.00594	0.0165	0.0330
8	*Micropogonias furnieri*	-0.226	0.0176	0.00290	-0.0939	-0.0149	-0.0612	-0.0215	0.0248	0.00418	0.0112	0.103
9	*Mugil* spp.	-0.00494	-0.0257	-0.00286	-0.00409	-0.00196	-0.0679	-0.00183	-0.000481	-0.00291	-0.00248	0.00148
10	*Trichiurus lepturus*	-0.0674	-0.0553	-0.000658	-0.0509	-0.00175	0.261	-0.00224	0.00592	-0.000575	0.000233	0.0509
11	Pelagic piscivorous	-0.00315	-0.0186	0.000056	0.000859	-0.000388	-0.00327	-0.000552	0.000934	0.000088	0.000267	-0.000646
12	Pelagic planktivorous	-0.223	0.0765	-0.00107	-0.0329	0.0608	0.261	0.0845	-0.137	-0.00558	-0.0342	0.00730
13	Pelagic opportunist	-0.318	-0.0966	-0.000306	0.00988	-0.0156	-0.0289	-0.0216	0.0363	0.000816	0.00865	-0.00357
14	Turtles	0	0	-0.000006	0	-0.000003	0.000001	-0.000004	0.000003	-0.000006	0.000002	-0.000001
15	Shrimp	0.00943	0.00779	-0.000541	-0.366	0.00257	-0.0441	0.00368	-0.00505	-0.000764	-0.00186	0.364
16	Crabs	0.00287	0.00294	0.000619	0.00188	-0.00348	0.00204	-0.00498	0.00585	0.000914	0.00251	0.000150
17	Squids	-0.0608	-0.223	-0.00173	-0.00288	0.00455	0,0151	0.00679	-0.00493	-0.00218	-0.00438	-0.000842
18	Benthos	-1.095	-1.120	-0.234	-0.718	1.323	-0.777	0.894	-2.230	-0.346	-0.962	-0.0590
19	Zooplankton	1.250	1.127	-0.0804	0.468	-1.150	0.849	-1.596	1.673	-0.000675	0.635	-0.0237
20	Primary Producers	0.288	0.405	0.894	0.193	-0.0762	0.145	-0.0969	0.304	-0.0540	0.00658	0.0959
21	Detritus	-0.0661	-0.146	-0.241	0.176	0.502	-0.105	0.465	-0.0343	-0.278	0	0.193
22	Fishery	0.0153	0.0127	-0.000259	-0.585	0.00427	-0.0705	0.00601	-0.00784	-0.000589	-0.00269	-0.417

Prebal – Pre balance model (North Bay Ecopath)

Table SM5. Rates to validate model: P/Q: Production/Consumption Rate (values must be between 0.1 and 0.3); Resp. /Ass.: Respiration/Assimilation rate (values need to be lower than 1.0); Resp./Biom.: Respiration/Biomass rate (values need to be from 1 to 10 for fish and from 50 to 100 for groups with higher turnovers rates). Values in bold do not attend the requisites.

Nr	Group name	P/Q	Resp./Ass.	Resp./Biom.
1	Dolphins	**0.006**	0.992	11.59
2	Seabirds	**0.008**	0.99	39.6
3	Benthopelagic opportunist	0.129	0.838	6.4
4	Demersal opportunist	0.121	0.848	5.462
5	Demersal piscivorous	**0.09**	0.888	7.951
6	Demersal zoobenthophagous	**0.408**	0.49	1.871
7	Catfish	**0.329**	0.589	1.155
8	*Micropogonias furnieri*	0.188	0.764	3.505
9	*Mugil* spp.	**0.037**	0.954	9.319
10	*Trichiurus lepturus*	0.116	0.855	2.275
11	Pelagic piscivorous	0.104	0.87	3.196
12	Pelagic planktivorous	0.182	0.773	7.268
13	Pelagic opportunist	0.272	0.659	6.054
14	Turtles	**0.059**	0.926	1.882
15	Shrimp	0.290	0.637	13.61
16	Crabs	**0.073**	0.908	13.864
17	Squids	0.159	0.801	9.116
18	Benthos	**0.355**	0.408	86.607
19	Zooplankton	0.25	0.583	56
20	Primary producers	-	-	-
21	Detritus	**-**	-	-

Phytoplankton

The concentration of Chlorophyll *a* is used as an index of phytoplankton biomass. Then, we used Chlorophyll *a* as an algal biomass indicator to estimate the primary producers's Standing crop for our North Bay food web model. We estimated the Biomass of the Standing Crop through remote sensoring using the MODIS Chlorophyll a layer (https://worldview.earthdata.nasa.gov/), which provides the near-surface concentration of chlorophyll a in milligrams of chlorophyll pigment per cubic meter (mg * m^{-3}) in the ocean. We took the average concentration of Chlorophyll a from 01st January 2014 through 31th Decembre 2015 (7.618 mg * m^{-3}). No data was available in MODIS for any subsequent period by the time our estimate was computed (i.e., February 2020). We may take two different ways to estimate the biomass of Standing Crop using Chlorophyll *a* concentration data. We explain in a step-by-step fashion the two aforementioned ways to estimate the Standing Crop biomass. The first way we can take is by converting Chlorophyll *a* concentration into Carbon weight fallowed by the conversion of Carbon weight into wet weight. The conversion factors we used assume that 1 mg C corresponds to 30 mg Chl a (Strickland 1960) and that 1 mg C corresponds to 10 mg WW (Dalsgaard & Pauly 1997). So we multiplied 7.618 by 30 to obtain the Carbon weight (228.554 mg C). Subsequently, we multiplied the aforementioned value by 10 to obtain the wet weight (2285.54 mg WW * m^{-3}). The second way we can take is by converting Chlorophyll *a* concentration into dry weight fallowed by the conversion of dry weight into wet weight. The conversion factors we used assume that 1 mg Chl a corresponds to 67 mg DW (APHA, 2012) and that 1 mg DW corresponds to 5 mg WW (Angelini et al. 2018). So we multiplied 7.618 by 67 to obtain dry weight (510.433 mg DW). Subsequently, we multiplied the aforementioned value by 5 to obtain the wet weight (2552.166 mg WW * m^{-3}). A practical and fast way to convert mg WW*m^{-3} to mg WW * m^{-2} (a suitable value for the Ecopath model) is to multiply the value in mg WW * m^{-3} by the depth of euphotic zone, which in the case of Norte Bay was assumed to be 3 m (Leonardo Rörig, pers. comm. 2020). Subsequently, we converted both values to t * km^{-2} units. Both results were similar. By converting through the first way the value found was 6.857 t * km^{-2}, while through the second way the value found was 7.656 t * km^{-2}. Thus, we chose the latter estimation as best biomass parameter value of the Primary producers group standing crop for our Norte Bay food web model. The primary productivity was taken from the Araça Bay food web model (Angelini et al. 2018), which was considered a similar ecosystems in terms of climate conditions.

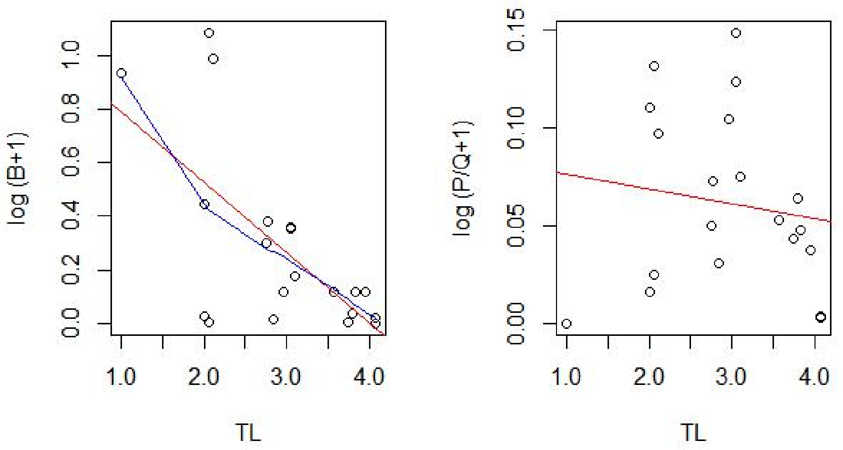

Fig. SM2. Prebal for North Bay Ecopath food web model. Relationships of Biomass (B) to Trophic Level (TL) and Production/Consumption Rates to TL.
log (B+1) = 0.9 - 0.218 * TL (response variable data with no normal distribution, Theil-Kendall method for non-parametric regression was used, slope's p-value < 0.001);
log (P/Q+1) = 0.084 - 0.007 * TL (data showing normal distribution, slope's p-value = 0.539).

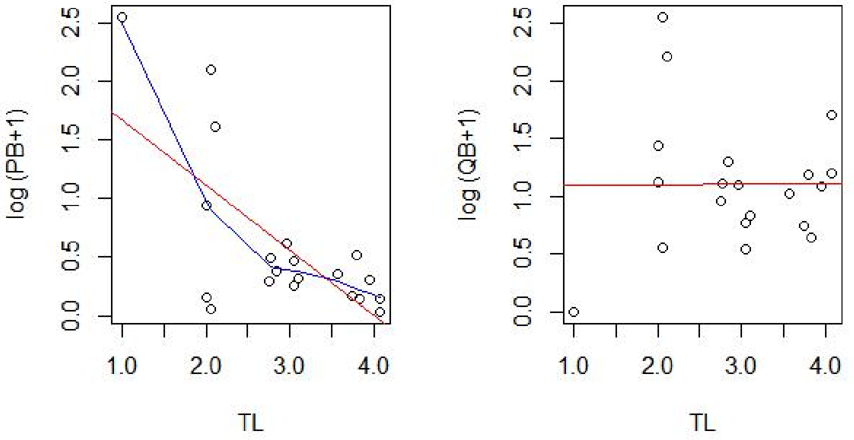

Fig. SM3. Prebal for North Bay Ecopath food web model. Relationships of Production/Biomass (PB) to Trophic Level (TL) and Consumption/Biomass (QB) to TL.
log (PB+1) = 1.451 - 0.332 * TL (response variable data distribution not normal, then the Theil-Kendall method for non-parametric regression was used, slope's p-value < 0.001);
log (QB+1) = 0.985 + 0.003 * TL (response variable data with normal distribution, slope's p-value = 0.985).

PARAMETERIZATION OF PB AND QB FOR FISH FUNCTIONAL GROUPS

In Ecopath, the Production rate (PB) is assumed to be equal to total mortality Z (Allen 1971), as shown below:

$$Z = F + M2 + M0 \tag{1}$$

where Z is the Total Mortality, F is the mortality due to fishing, M2 is the natural mortality due to predation, and $M0$ is other mortality (due to old age, deceases, etc.). Thus, we can estimate the natural mortality (M) from an empirical relationship that links M, the parameters of the von Bertalanffy Growth Function (VBGF), to mean environmental temperature (Pauly 1980) as follow:

$$\log M = \log PB = \ 0.9849 \ * K^{0.65} * L_{\infty}{}^{-0.297} \ * T^{0.463} \tag{2}$$

where, M is the natural mortality (year^{-1}), K is the curvature parameter of the VBGF (year^{-1}), L_{∞} is the asymptotic length in cm, T is the mean environmental temperature, in °C. A life-history routine FishBase (Froese & Pauly 2017) was used to estimate M, L_{∞} being assumed to equal L_{max}. K was determined using known relationships between L_{∞} and K within the FishBase life-history routine. The mean sea surface temperature in the North Bay was assumed to be 22.5 °C (Simonassi et al. 2010). When functional groups comprised several species, the group PB was estimated as a weighted average (weighted by each species biomass).

Consumption rates (QB) of fish species were estimated from empirical formulae implemented in the life-history routine of FishBase (Froese & Pauly 2017), derived by Palomares & Pauly (1998) as follows:

$$log\, QB = \ 7.964 \ - \ 0.204 * \ \log W_{\infty} \ - \ 1.965\, T' \ + \ 0.083 \ * \ Ar + \ 0.532 \ * \ H \ + \ 0.398 \ * \ D \tag{3}$$

where Z is total mortality, W_{∞} is the asymptotic weight (g), T' is the mean annual temperature (expressed using T' = 1,000/Kelvin (Kelvin = °C + 273.15), Ar is the aspect ratio (height^2 (cm)/surface area (cm) of the caudal fin), h is a dummy variable expressing trophic category (1 for herbivores, and 0 for detritivores and carnivores), and d is a dummy variable also expressing food type (1 for detritivores, and 0 for others than detritivores). For cases where Z is not available, the following relation may be used:

$$logQB = 7.964 + (0.204 * \log W_{\infty}) - \left(1.965T^{'}\right) + (0.083 * Ar) + (0.532 * h) + (0.398 * d) \quad (4)$$

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CONCLUSÃO GERAL

Com respeito à metodologia utilizada, foi possível corroborar nesta Tese que a modelagem ecológica com Ecopath e as ferramentas atualmente disponíveis para a análise de redes tróficas, tais como a ENA, são ferramentas de grande potencial para a avaliação e quantificação da natureza e força das interações biológicas entre componentes de uma teia trófica e a consequente determinação do papel ecológico das espécies. As duas ferramentas utilizadas nesta Tese (Ecopath e ENA) podem ser utilizadas de maneira complementar para tal fim.

Com relação à função ou papel ecológico dos mamíferos marinhos no mundo, os resultados desta Tese contribuem à teoria ecológica. Foi possível concluir que:

➢ Embora os mamíferos marinhos sejam espécies-chaves em muitos ecossistemas, a natureza e força das interações e o papel ecológico de um determinado grupo trófico de mamífero marinho em um determinado ecossistema é peculiar para cada caso específico. Não foi detectada diferenciação nem padrão algum no papel ecológico dos principais grupos de mamíferos marinhos ao longo do gradiente latitudinal, nem mesmo entre diferentes tipos de ecossistemas. Ou seja, a magnitude do papel ecológico de um determinado grupo trófico de mamífero marinho não pode ser previsto ou predito, embora esteja influenciado pela posição trófica e pela biomassa para odontocetos e pinípedes.

➢ Os resultados desta Tese mostram que de maneira geral (isto é, para todos os grupos taxonômicos avaliados na modelagem estatística), quanto maior o nível trófico das presas consumidas pelos mamíferos marinhos, maior é o impacto trófico associado. Isto se deve a que quanto maior for o nível trófico das presas, maior a probabilidade de ocorrer cascatas tróficas e efeitos indiretos.

➢ Com exceção dos misticetos, quanto maior a biomassa, maior o impacto trófico dos mamíferos marinhos. A biomassa de um grupo dado é diretamente proporcional à abundância e ao porte da espécie. Por sua vez, o porte do animal está associado à taxa de consumo (quanto maior o porte, menor a sua taxa de consumo). Entretanto, a taxa de consumo não tem efeito sobre o impacto trófico do animal, logo o aumento do impacto trófico associado a um aumento da biomassa não depende do porte do animal, mas sim da sua abundância. Isto significa que a diminuição na abundância (com a sua consequente perda de biomassa) de odontocetos e pinípedes pode causar mudanças profundas na estruturação dos ecossistemas por estes animais.

Já no caso específico do boto-cinza (*Sotalia guianensis*) da Baia Norte de Santa Catarina, pôde-se concluir que:

- A conservação do boto-cinza é essencial para o manejo do ecossistema da Baía Norte de Santa Catarina. Os resultados desta Tese mostram os botos como uma espécie-chave no ecossistema. Isto significa que os botos apresentam o maior impacto trófico por unidade de biomassa entre todos os compartimentos considerados no modelo trófico da Baía Norte. Em outras palavras, apesar de a sua biomassa ser menor que a de outros compartimentos, os botos desempenham um papel essencial na estruturação da teia trófica da Baía Norte de Santa Catarina, tendo sido detectado vários casos de mutualismo entre os botos e algumas das suas presas.
- Os botos podem ser o compartimento mais vulnerável à remoção de outros compartimentos no ecossistema da Baia Norte de Santa Catarina. Apesar do seu papel preponderante no ecossistema, os botos são o compartimento que mais depende de outros compartimentos para a obtenção de biomassa. Isto tem implicações com a vulnerabilidade dos botos, uma vez que, quanto maior for a dependência de um dado compartimento com relação a outros compartimentos doadores de matéria-energia, maior sua vulnerabilidade perante possíveis perturbações, tais como a remoção de compartimentos.
- O manejo da corvina (*Micropogonias furnieri*) é essencial para o ecossistema da Baía Norte. A corvina é a principal presa consumida pelos botos e por algumas espécies de aves marinhas, além de ser a principal espécie de peixe alvo da pesca no ecossistema. Contudo, apesar de esta espécie ser importante para esses predadores de topo e para a pesca, os resultados desta Tese mostram que a corvina é um compartimento central para todo o ecossistema, sendo que este compartimento mostra a maior quantidade de fluxos da teia trófica. Isto significa que o manejo da corvina, enquanto recurso pesqueiro, é crucial para os botos, mas também para o ecossistema como um todo.

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