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ESTRUTURA E DINÂMICA DE UMA REDE TRÓFICA MARINHA NEOTROPICAL: UMA PONTE ENTRE A TEORIA DE REDES E AS ESTRATÉGIAS DE CONSERVAÇÃO

João Pessoa
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Orientador: Prof. Dr. Ricardo de Souza Rosa
Segundo orientador: Dr. Andrés Felipe Navia
Co-orientador: Prof. Dr. Rafael L.G. Raimundo

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defendida e aprovada em 28/07/2021 pela seguinte banca examinadora:

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Ata da 141ª Apresentação e Banca de Defesa de Doutorado de Viviana Márquez Velásquez

Ao(s) Vinte e oito dias do mês de julho de dois mil e vinte e um, às 09:00 horas, no(a) Ambiente Virtual, da Universidade Federal da Paraíba, reuniram-se, em caráter de solenidade pública, membros da banca examinadora para avaliar a tese de doutorado de **Viviana Márquez Velásquez**, candidato(a) ao grau de Doutor(a) em Ciências Biológicas. A banca examinadora foi composta pelos seguintes membros: **Dr.Ricardo de Souza Rosa (Orientador- UFPB/PB); Dra.Cecilia Andreazzi (FIOCRUZ); vDr. Mathias Mistretta Pires (UNICAMP/SP); DraPaula Lemos -Costa (Universidade de Chicago); vDra. Priscila Lopes (UFRN/RN). Compareceram à** solenidade, além do(a) candidato(a) e membros da banca examinadora, alunos e professores do PPGCB. Dando início à sessão, a coordenação fez a abertura dos trabalhos, apresentando o(a) discente e os membros da banca. Foi passada a palavra ao(à) orientador(a), para que assumisse a posição de presidente da sessão. A partir de então, o(a) presidente, após declarar o objeto da solenidade, concedeu a palavra a **Viviana Márquez Velásquez**, para que dissertasse, oral e sucintamente, a respeito de seu trabalho intitulado **"ESTRUTURA E DINÂMICA DE UMA REDE TRÓFICA MARINHA TROPICAL: UMA PONTE ENTRE A TEORIA DE REDES E ESTRATÉGIAS DE CONSERVAÇÃO".** Passando então a discorrer sobre o aludido tema, dentro do prazo legal, o(a) candidato(a) foi a seguir arguido(a) pelos examinadores na forma regimental. Em seguida, passou a Comissão, em caráter secreto, a proceder à avaliação e julgamento do trabalho, concluindo por atribuir-lhe o conceito **APROVADO**. Perante o resultado proclamado, os documentos da banca foram preparados para trâmites seguintes. Encerrados os trabalhos, nada mais havendo a tratar, eu, orientador(a), como presidente, lavrei a presente ata que, lida e aprovada, assino juntamente com os demais membros da banca examinadora.

João Pessoa, 28/07/21.

Ricardo S Rosa

Orientador(a)

Examinador(

Examinador(a)

Mathias

Examinador(a)

Priscila F. M Lopes

Examinador(a)

Viviana Marquez Velásquez

Viviana Márquez Velásquez
(discente ciente do resultado)

(Em modo de webconferência, as assinaturas digitalizadas são certificadas pelo presidente da banca)

DEDICATORIA

A toda mi familia,

Especialmente a mi mamá, por tanto amor, confianza y por ser mi base,

Al Papá, por su ejemplo de fortaleza,

A la tía Monja que siempre me dio tantas y tantas oportunidades y me abrió tantos caminos,

A mis hermanos y sobrinos, por el apoyo, cariño

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RESUMO

Os ecossistemas marinhos costeiros enfrentam fortes impactos em num ritmo sem precedentes no Antropoceno, tais como a poluição, a introdução de espécies exóticas, a mudança climática e a sobrepesca. A sobrepesca erode a biodiversidade marinha e o funcionamento dos ecossistemas, pois afeta as interações entre as espécies, as suas abundâncias e diversidade de traços, e em última instância, os serviços ecossistêmicos. Os avanços na teoria de redes ecológicas podem nos ajudar a avaliar e mitigar os impactos antropogênicos sobre a biodiversidade marinha. Por exemplo, análises estruturais de redes podem descrever padrões de interações de espécies, que representam conexões fundamentais entre a arquitetura da biodiversidade e as funções do ecossistema, e também informar o papel estrutural e funcional que cada espécie desempenha na comunidade ecológica. Além disso, a modelagem e simulações de redes podem fornecer previsões teoricamente fundamentadas de como a perda de biodiversidade pode remodelar propriedades no nível comunitário, tais como resiliência, robustez e diversidade funcional, e influenciar a persistência a longo prazo dos ecossistemas. Particularmente, os modelos de redes adaptativas permitem prever mudanças dinâmicas que surgem da reconfiguração das interações das espécies impulsionadas pelas extinções, juntamente com vários outros processos ecológicos e evolutivos. Uma rede adaptativa é definida pelos efeitos mútuos entre as mudanças nos padrões de interação e as propriedades associadas da rede que caracterizam a estrutura e a dinâmica da comunidade, tais como aninhamento, modularidade e estabilidade; e no nível populacional, os processos eco-evolutivos que moldam as propriedades das espécies, tais como as abundâncias e valores dos traços. Nesta tese, aplicamos a abordagem de redes para fazer a ponte entre a teoria da ecologia de comunidades a e a conservação da biodiversidade marinha baseada em evidências. Seguimos três passos para isto. No primeiro capítulo, exploramos e discutimos como a abordagem de redes ecológicas é utilizada para compreender como está estruturada a biodiversidade marinha, e para prever a resposta das redes tróficas às estratégias de manejo e gestão, como a redução da pressão da pesca. Nesse capítulo apresentamos novas perspectivas teóricas e metodológicas que permitem fazer a ponte entre modelos de redes adaptativas, grandes bases de dados de interação de espécies, e experimentos em campo, a fim de construir uma interface que garanta fluxos de conhecimento multidirecionais entre modelos teóricos de rede, ecologia marinha experimental e políticas e práticas de conservação no Oceano Pacífico tropical. No segundo capítulo descrevemos a estrutura de uma rede trófica rica em espécies na costa do Pacífico colombiano, descrevendo os papéis topológicos de mais de 300 espécies junto com a pesca artesanal e industrial, e identificando alguns hubs de rede, hubs de módulos e entidades conectoras (pesca e espécies) que realizam mais de 1000 interações tróficas em toda a rede. Discutimos a baixa similaridade das interações entre estes hubs da rede em termos de partição de recursos, a qual seria o reflexo do fantasma da competição passada imposta por décadas de pesca intensiva. Em termos de priorização da conservação, nossas análises identificam duas espécies de tubarão-martelo (*Sphyrna lewini* e *S. media*) cuja centralidade na rede os torna qualitativamente comparáveis à pesca artesanal como hyper-hubs - um conceito que propomos aqui para definir hubs da rede altamente centrais que predam outros hubs da rede e que, portanto, podem exercer efeitos *top-down* muitos amplos na rede trófica. Simulações de extinção de espécies com papéis topológicos variados, incluindo *hyper-hubs*, e considerando os níveis tróficos, não mudaram a estrutura modular da rede trófica nem as frequências relativas dos papéis topológicos. Entretanto, estas simulações mudam a identidade das espécies por papel topológico, com várias espécies de tubarões *Sphyrna* surgindo recorrentemente como hubs de rede, reforçando a noção de que uma alta prioridade de conservação deve ser dada às mesmas. Finalmente, no terceiro capítulo, desenvolvemos um primeiro modelo de rede adaptativa para investigar se nossas previsões a respeito dos efeitos da regulação da pesca e perda de espécies se mantêm sob a reconfiguração adaptativa das interações, ou seja, à medida que as espécies ajustam suas interações após as extinções e os feedbacks das interações-abundâncias e traços. Estes primeiros resultados mostraram que a reconfiguração de interações e a intensidade da pesca podem agravar as consequências da perda de espécies, possivelmente desencadeando cascatas de extinção que afetam a resiliência e causam fortes mudanças na dinâmica da rede trófica marinha costeira. Estes modelos de rede são baseados na síntese entre as teorias ecológicas e evolutivas e, portanto, podem melhorar em grande medida a nossa capacidade de compreender e prever os resultados de distúrbios antropogênicos nas comunidades dos ecossistemas marinhos costeiros.

Palavras-chave: competição, conservação, engenharia da biodiversidade, pesca, redes ecológicas marinhas, teoria de redes

ABSTRACT

Coastal marine ecosystems experience strong impacts in an unprecedented rate in the Anthropocene, such as pollution, introduction of alien species, climate change and overfishing. Overfishing erodes marine biodiversity and ecosystem functioning as it affects species interactions, abundances, trait diversity and ultimately ecosystem services. Advances in ecological network theory can help us to assess and mitigate anthropogenic impacts on marine biodiversity. For example, structural network analyses can describe patterns of species interactions, which represent fundamental connections between the architecture of biodiversity and ecosystem functions, and also inform the structural and functional role that each species plays in an ecological community. Additionally, network modeling and simulations can provide theoretically founded predictions of how biodiversity loss is expected to reshape community-level properties, such as resilience, robustness, and functional diversity, and influence the long-term persistence of ecosystems. Particularly, adaptive network models can predict dynamic changes that arise from interaction rewiring -the reconfiguration of species interactions driven by extinctions alongside with several other ecological and evolutionary processes. An adaptive network is defined by the mutual effects between changes in interaction patterns and associated network properties that characterize community structure and dynamics, such as nestedness, modularity, and stability; and population-level, eco-evolutionary processes shaping the properties of species that form the network, such as their abundances and trait values. In this thesis, we apply the network approach to bridge ecological community theory and evidence-based conservation. We followed three steps towards the inception of network theory into evidence-based conservation strategies for marine biodiversity. In the first chapter, we explored and discussed how the ecological network approach is used to understand the structure of marine biodiversity, and to predict the response of trophic networks to management strategies such as reducing fishing pressure. In this the chapter we introduced novel theoretical and methodological perspectives that now allow us to bridge adaptive network models, species-interaction "big data" and field experiments, in order to build an interface ensuring multidirectional knowledge flows among theoretical network models, experimental marine ecology, and conservation policies and practices in the tropical Pacific Ocean. In the second chapter, we described the structure of a species-rich food web in the Colombian Pacific coast, unravelling the functional roles of more than 300 species alongside with small- and large-scale fisheries, identifying some network hubs, module hubs and connectors entities (fisheries and species) that drive up to 1,100 trophic interactions over the entire network. We discuss the high degree of interaction dissimilarity among network hubs in terms of resource partitioning that would be the ghost of past competition imposed by decades of intensive fisheries. In terms of conservation prioritization, our analyses identify two hammerhead shark species (*S. lewini* and *S. media*) whose centrality in the network make them qualitatively comparable to small-scale fisheries as hyper-hubs -- a concept that we propose here to define highly central network hubs that prey on other network hubs and hence are likely to exert amplified top-down effects over the entire food web. Simulations of single-species extinctions with varying topological roles, including hyper-hubs, and trophic levels did not change the overall architecture of the food web nor the relative frequencies of topological roles. However, simulated extinctions often change the species identities within topological roles, with several *Sphyrna* species recurrently emerging as network hubs, reinforcing the notion that a high conservation priority should be given to them. Finally, in the third chapter, we developed an adaptive network model to investigate if our predictions regarding the effects of fisheries regulation and species losses hold on under adaptive rewiring, i.e., as species adjust their interactions following extinctions and the trait-interaction-abundance feedbacks that they trigger. These first results have shown that the rewiring and fishery strength may potentially aggravate the consequences of loss of species, and possibly trigger extinction cascades affecting the resilience and causing strong changes in the dynamics of the coastal marine food web. These network models are founded on the ongoing synthesis between ecological and evolutionary theories and hence can greatly improve our ability to understand and predict community-wide outcomes of anthropogenic disturbances in coastal marine ecosystems.

Keywords: competition, conservation, biodiversity engineering, tropical marine fishes, marine ecological networks, network theory

SUMÁRIO

APRESENTAÇÃO

APRESENTAÇÃO

Esta tese está dividida em três capítulos, na forma de artigos, em inglês. O primeiro capítulo foi publicado como capitulo do livro *Marine Coastal Ecosystems Modelling and Conservation*, da editora Springer (DOI: 10.1007/978-3-030-58211-19). O segundo capítulo foi aceito para publicação na revista *ICES Journal of Marine Science.* Finalmente o terceiro capítulo será submetido para publicação na revista *Ecological Modelling*, após os ajustes necessários depois da banca.

INTRODUÇÃO GERAL

A acelerada mudança na biodiversidade devido aos impactos humanos é uma característica acentuada do Antropoceno (Barnosky, 2011; McCauley et al., 2015), com consequências drásticas para o funcionamento dos ecossistemas e os serviços providos para a humanidade (Chapin et al., 2000; Díaz et al., 2006).

Os diferentes serviços ecossistêmicos proporcionados ao homem fazem parte de sistemas socioecológicos complexos, os quais abrangem subsistemas tais como o sistema de recursos, como a pesca costeira; as unidades de recursos como as espécies de peixes; os usuários como os pescadores; e o sistema de governança como as organizações e regras que regem a pesca costeira. Estes subsistemas são relativamente separáveis e interagem uns com outros (Ostrom, 2009). Os ecossistemas marinhos, os quais proveem aos seres humanos serviços ecossistêmicos essenciais como a produção de alimentos (Costanza et al., 1997), enfrentam diversas pressões antropogênicas em diferentes escalas espaciais e temporais, que modificam os padrões de riqueza de espécies, as suas abundâncias, as suas interações, e as funções ecossistêmicas associadas. Tais pressões incluem modificação do habitat (Bulleri & Chapman, 2010; Heery et al., 2017), poluição (Nixon, 1995; Islam & Tanaka, 2004), a introdução de espécies exóticas (Vitousek et al., 1997; Bax et al., 2003), mudanças climáticas (Hoegh-Guldberg & Bruno, 2010; Hillebrand et al., 2018) e a sobrepesca (Jackson et al., 2001; Hsieh et al., 2006; McCauley et al., 2015; Pauly & Zeller, 2016). Localmente, a sobrepesca é um motor crítico de extinção de espécies nativas através do qual são induzidas mudanças nos padrões de interação das espécies e na estabilidade das comunidades, ameaçando assim a persistência a longo prazo das redes tróficas marinhas (Jennings & Kaiser, 1998; Lotze et al., 2011; Gilljam et al., 2015; Bell et al., 2018) e a segurança alimentar das comunidades que dependem da atividade pesqueira (FAO, 2020). Tais sistemas socioecológicos exigem pesquisas que combinem conhecimentos da ciência ecológica e social para aumentar os esforços para a sua sustentabilidade (Ostrom, 2009).

A pesca é uma importante atividade econômica em muitos países, assim como uma fonte crucial de emprego e renda para milhões de pessoas (Dyck & Sumaila, 2010; Teh & Sumaila, 2011; FAO, 2018). Nos países em desenvolvimento, principalmente na região tropical, a pesca é crucial para a segurança alimentar das comunidades costeiras (Kent, 1997; Béné et al., 2010; FAO, 2020). Muitas destas comunidades, que dependente principalmente da pesca artesanal, enfrentam pobreza persistente, insegurança alimentar e o declínio de recursos pesqueiros (Mills et al., 2011; Purcell & Pomeroy 2015). A pesca artesanal nas regiões tropicais geralmente é complexa de gerenciar, devido a seu caráter multiespecífico e de múltiplas redes (Berkes et al., 2001); além de estar ligada à dinâmica dos ecossistemas costeiros e recifais (Hawkins & Roberts, 2004; Batista et al., 2014), os quais são simultaneamente impactados por fatores de estresse local e global (Hoegh-Guldberg et al., 2007). Assim, a compreensão e gestão dos processos antropogênicos e ecológicos que moldam a biodiversidade dos ecossistemas marinhos e as suas redes tróficas, é fundamental para garantir a segurança alimentar das populações humanas e conservar a biodiversidade e as funções dos ecossistemas (Worm et al., 2006; Lotze et al., 2011; Dunne et al., 2016).

Abordagem de Redes para análises da biodiversidade

Durante as últimas décadas, a abordagem de redes para o estudo de sistemas naturais complexos (Barabási, 2016) tem sido amplamente aplicada em Ecologia, permitindo a descrição e análises comparativa da estrutura das comunidades, em relação aos padrões de interação das espécies (e.g., Dunne et al., 2002; Olesen et al., 2007; Borthagaray et al., 2014; Saravia et al., 2018). Ademais permitem identificar os papéis topológicos que as espécies desempenham dentro das redes, e assim, saber como influenciam a propagação dos efeitos ecológicos e evolutivos (e.g., Guimerà & Amaral, 2005; Jordán et al., 2006; Olesen et al., 2007; Jordán, 2009; Andreazzi et al., 2017); e explorar os mecanismos ecológicos e evolutivos que moldam as interações ecológicas entre as espécies (e.g., Rezende et al. 2009; Suweis et al., 2013; Poisot et al., 2015). Como as redes de interação de espécies capturam a relação entre a biodiversidade e as funções dos ecossistemas, podem ser ferramentas valiosas para prever os efeitos das perturbações naturais ou antropogênicas na dinâmica da biodiversidade (Dunne et al., 2002, 2004; Pérez-Matus et al., 2017; Vinagre et al., 2019; Márquez-

Velásquez et al., unpublished data).

Recentemente, a integração entre teorias ecológicas e evolutivas, os avanços metodológicos que envolvem uma diversidade de análises estruturais (e.g., Guimerà & Amaral, 2005; Jordán et al., 2006; Olesen et al., 2007) e de modelagem de redes (e.g., Allesina & Tang, 2015; Andreazzi et al., 2017) e a disponibilidade de grandes bases de dados sobre biodiversidade, estão sustentando quadros de previsão abrangentes para testar hipóteses teoricamente informadas sobre como as mudanças induzidas pelo homem na composição das biotas locais influenciam propriedades-chave da comunidade, tais como a robustez, resiliência, estabilidade e a diversidade funcional (Dunne et al., 2004; Evans et al., 2013; Kéfi et al., 2016; Raimundo et al., 2018a). Atualmente, novas abordagens de modelagem de redes estão sendo aplicadas para avaliar os processos eco-evolutivos que moldam padrões de redes ecológicas (e.g., Andreazzi et al., 2017, 2018; Raimundo et al. 2018b). Esta integração de linhas de pesquisa constitui um passo fundamental para avançar no entendimento teórico sobre a relação entre a estrutura e a dinâmica ecológica e evolutiva da biodiversidade (Loeuille & Loreau, 2005; Ings et al., 2009; Thébault & Fontaine, 2010; Rohr & Bascompte, 2014; Yen et al., 2016; Andreazzi et al., 2017, 2018; Raimundo et al. 2018b).

Nos últimos anos é crescente o número de pesquisas que usam a abordagem de redes para explorar efeitos antropogênicos, tais como a pesca ou a caça, sobre a biodiversidade nos ecossistemas marinhos, particularmente no que diz respeito às consequências da extinção de espécies (Navia et al., 2010, 2012; Dunne et al., 2016; Pérez-Matus et al., 2017; Vinagre et al., 2019; Ávila-Thieme et al., 2020). Assim, compreender e prever como as redes de interação estão estruturadas e como respondem às diversas perturbações antropogênicas, é fundamental para o desenho de estratégias baseadas em processos, com o objetivo de subsidiar estratégias de conservação e restauração da biodiversidade (Raimundo et al. 2018a).

Estrutura das redes tróficas marinhas e funções topológicas das espécies

Assim como outras comunidades ecológicas ricas em espécies cuja estrutura e dinâmica são governadas pelos efeitos das interações das espécies, as redes tróficas marinhas podem ser descritas e compreendidas em termos dos seus padrões estruturais (Dunne et al., 2004; Pascual & Dunne 2006; Ings et al., 2009; Rezende et al., 2009; Navia et al., 2016). As redes tróficas marinhas, exibem padrões estruturais recorrentes, como o padrão Modular (Newman & Girvan, 2004). A modularidade ocorre quando um subconjunto de espécies interage mais frequentemente entre si do que com as outras espécies da rede (Newman & Girvan, 2004). A teoria prevê que a estrutura modular pode aumentar a estabilidade nas redes tróficas (May, 1972, 1973; Pimm, 1979; Thébault & Fontaine, 2010; Stouffer & Bascompte, 2011) ao impedir o impacto e a propagação das perturbações, seja porque as perturbações permaneçem dentro de um único compartimento, ou seja porque atingem com magnitudes reduzidas outros compartimentos (Krause et al., 2003). Este padrão estrutural modular tem sido identificado na região do Ártico (Kortsch et al., 2015), do Antártico (Saravia et al., 2018), em regiões temperadas (Krause et al., 2003; Pérez-Matus et al., 2017) e em redes tróficas marinhas tropicais (Rezende et al., 2009). Na região tropical, espécies de tubarões filogeneticamente relacionadas e de níveis tróficos diferentes, tenderam a ocupar módulos diferentes, sugerindo que a competição pode desempenhar um papel importante na estruturação destes compartimentos (Rezende et al., 2009). Porém, apesar do papel recorrente da modularidade como um importante motor da biodiversidade marinha, uma visão abrangente deste padrão estrutural e seus efeitos nas dinâmicas ecológicas e evolutivas das redes tróficas marinhas ainda está em falta.

Uma vez identificado o padrão modular para uma determinada rede trófica, é possível caracterizar os papéis topológicos que as espécies desempenham na rede. Neste texto, o termo papel topológico refere-se ao padrão de conectividade que descreve o equilíbrio entre a distribuição das interações de uma espécie entre e dentro dos módulos (Guimerà & Amaral, 2005; Olesen et al., 2007; Borthagaray et al., 2014; Saravia et al., 2018).

A tipologia estabelecida dos papéis topológicos dentro das redes modulares engloba quatro categorias: (i) hubs de rede, que são espécies que exibem simultaneamente alto grão de conectividade intra e intermodular, ou seja, são espécies que constituem as pedras angulares da estrutura da rede e de cuja remoção se espera gerar amplas consequências estruturais e dinâmicas; (ii) hubs de módulos, que são espécies que exibem baixa conectividade intermodular mas alta conectividade intramodular, ou seja, estas espécies são os motores da estrutura e dinâmica local mas sem um impacto topológico global; (iii) conectores, são espécies que exibem alta conectividade intermodular mas baixa conectividade intramodular, ou seja, estas espécies são relevantes porque podem ser ligações únicas entre grandes módulos, mesmo que tenham um baixo número de ligações; (iv) periféricos, são espécies com baixa conectividade intra e intermodular e, portanto, espera-se que tenham um impacto mínimo na estrutura e dinâmica da comunidade (Guimerà & Amaral, 2005; Olesen et al., 2007).

Os papéis topológicos são principalmente determinados por características das espécies que influenciam as interações ecológicas, tais como abundância, amplitude de nicho, motilidade, e posições tróficas, juntamente com propriedades específicas da comunidade, como o *clustering* filogenético (Rezende et al., 2009, Guimerà et al., 2010; Borthagaray et al., 2014; Olmo-Gilabert et al., 2019), as quais restringem os padrões de interação e as possíveis reconfigurações das interações. Os papéis topológicos das espécies representam um proxy informativo da contribuição de uma espécie para a estrutura e para a dinâmica da comunidade. É importante notar que os papéis topológicos mudam ao longo do tempo devido a uma variedade de mecanismos que moldam a conectividade das espécies, incluindo a substituição temporal delas (Díaz-Castelazo et al., 2013) e vários mecanismos adaptativos de reconfiguração de interações (Valdovinos et al., 2010; Ramos-Jiliberto et al., 2012; Raimundo et al. 2018a).

Mecanismo que moldam a estrutura das redes tróficas marinhas

Vários mecanismos têm sido propostos para explicar os padrões estruturais das redes tróficas. Entre estes mecanismos encontram-se: os i) processos baseados em traços (Cohen et al., 1993; Laigle et al., 2018, Webb et al., 2002; Cattin et al., 2004; Rezende et al., 2009), e ii) os processos neutros decorrentes da variação espaço-temporal da distribuição de abundâncias (Cohen et al., 2003; Vásquez et al., 2007). Os efeitos recíprocos entre os processos baseados em traços e os processos neutros, formam um ciclo de feedbacks entre a dinâmica ecológica e evolutiva, os chamados processos eco-evolutivos, que conectam dinamicamente os padrões de interação, a estabilidade da comunidade e a diversidade funcional (ver Raimundo et al., 2018a e as respectivas referências; Segar et al., 2020). As interações recíprocas entre estes processos permitem aos organismos, em escalas de tempo contemporâneas, tanto moldar como adaptar-se ao seu ambiente (Levins, 1968; Hairston et al., 2005; Beck et al., 2012, Travis et al., 2014; Peralta et al., 2015). Assim, as dinâmicas ecológicas fornecem o contexto para a mudança evolutiva (Thompson, 1998; Grant & Grant, 2002; Post & Palkovacs, 2009; Shoener, 2011; Hendry, 2017), e vice-versa (Fussmann et al., 2007; Urban et al., 2008; Pelletier et al., 2009; Matthews et al., 2011).

Nos últimos anos os efeitos dos impactos das atividades humanas e das críticas mudanças ambientais nas interações das espécies estão sendo cada vez mais estudadas (e.g., Woodward et al., 2010; Lotze, et al., 2011; Kortsch et al., 2015; Bartley et al., 2019). Entretanto o grau em que as redes podem responder às pressões antrópicas e ambientais através da reconfiguração das interações e das mudanças nas abundâncias e nos traços das espécies ao longo do tempo, permanecem ainda pouco exploradas, principalmente para redes tróficas de ambientes marinhos (Hanski, 2012).

Atualmente enfrentamos o desafio de construir teorias e previsões gerais sobre como os mecanismos eco-evolutivos influenciam as dinâmicas das redes tróficas de ambientes marinhos sob pressões derivadas de atividades humanas, considerando que as abundâncias e os traços podem variar amplamente no espaço e no tempo e que podem ser influenciados por processos que ocorrem em diferentes níveis de organização biológica, como genes, indivíduos, populações, comunidades e ecossistemas (Pacheco et al., 2006). Assim, compreender e prever como os processos evolutivos interagem com a estrutura e persistência das redes tróficas marinhas, desempenhará um papel chave no entendimento e na gestão dos impactos destas mudanças nos ecossistemas marinhos tropicais.

Neste contexto, as redes adaptativas (Gross & Blasius, 2008; Gross & Sayama, 2009) representam uma promissora ferramenta de modelagem que permite abordar os feedbacks entre as interações das espécies, as abundâncias e os traços (Poisot et al., 2015). Neste tipo de modelos dinâmicos a variação temporal dos padrões de interação devido às reconfigurações das interações (a dinâmica macroscópica da topologia da rede), retroalimenta-se com a dinâmica das populações das espécies (a dinâmica microscópica, dos nós da rede). Assim, as alterações na topologia da rede reestruturam as propriedades no nível populacional das espécies, tais como traços e abundâncias. Inversamente, os padrões emergentes de traços e abundâncias conduzem a novas alterações nos padrões de interações tróficas, definindo esses ciclos de *feedbacks* eco-evolutivos. A reconfiguração das interações tróficas após alguma pressão antrópica como a pesca, será frequentemente condicionada por traços morfológicos, comportamentais ou fenológicos que impõem restrições às interações e geram interações proibidas, ou seja, interações entre espécies coexistentes que nunca ocorrerão devido a incompatibilidades biológicas entre elas (Jordano et al., 2003; Olesen et al., 2011; Strona & Veech, 2017).

Assim, as redes adaptativas representam uma abordagem integradora da investigação teórica e empírica sobre a dinâmica das comunidades marinhas que estão sob intensa pressão antrópica, promovendo o desenho de experimentos em campo que permitam testar hipóteses-chave para ajustar as estratégias de conservação e restauração (Raimundo et al., 2018a).

A pesca nas redes tróficas marinhas

A atividade pesqueira, dependendo da sua intensidade, pode ter efeitos drásticos sobre os ecossistemas marinhos, impondo mudanças nas interações das espécies com amplos efeitos no nível comunitário. Tais efeitos alteram a distribuição das abundâncias das espécies (Myers et al., 1996), a sua diversidade genética (Pinsky & Palumbi, 2014), e os traços, os quais podem determinar as interações ecológicas (Jennings et al., 1999; Bianchi et al., 2000; Edeline & Loeuille, 2020). Portanto, a perda de espécies induzidas pela pesca, pode reconfigurar a estrutura e a dinâmica das redes de interação de espécies (Bascompte et al., 2005; Myers et al., 2007; Dunne et al., 2016; Pérez-Matus et al., 2017) com repercussões na composição da comunidade (Hutchings & Baum, 2005) e na estrutura trófica (Pauly et al., 1998; Ferretti et al., 2010), tais como reportadas para os ecossistemas em regiões temperadas (Shepherd & Myers, 2005; Myers et al., 2007; Gaichas & Francis 2008; Coll et al., 2009; Ávila-Thieme et al., 2020) e tropicais (Stevens et al., 2000; Navia et al., 2012, 2016).

Nos ecossistemas marinhos a pesca pode comportar-se como um forrageador adaptativo, ao procurar otimizar as taxas de captura das espécies alvo (Begossi, 1992; Bertrand et al., 2007; Poos & Rijnsdorp, 2007) e com a possibilidade de mudar o alvo visando maximizar os lucros (Acheson, 1988; Sethi et al., 2010). Tais padrões dinâmicos da pesca (Tromeur & Loeuille, 2018) podem desencadear *feedbacks* eco-evolutivos que se propagarão pela comunidade e reconfigurarão a abundância das espécies, a distribuição de traços (Barraclough, 2015) e os seus padrões de interação (Palkovacs et al., 2012; Ávila-Thieme et al., 2020). Alguns autores argumentam que a captura adaptativa da pesca pode estabilizar a dinâmica das comunidades, uma vez que redistribui dinamicamente as pressões de predação sobre as espécies de presas mais abundantes (Kondoh, 2003; Loeuille, 2010). Por outro lado, tais alterações adaptativas poderiam induzir mudanças de fase abruptas com consequências inesperadas para a estrutura e dinâmica da comunidade (Jackson et al., 2001; Estes et al., 2011, 2016; Conversi et al., 2015).

Para esclarecer previsões conflitantes existentes sobre os impactos da pesca sobre a rede, é importante que a pesca seja incorporada nas análises das redes tróficas como um nó adicional, o qual seria análogo ao nó dos predadores (Dunne et al., 2016; Pérez-Matus et al., 2017; Glaum et al., 2020; Ávila-Thieme et al., 2021), já que seus padrões de interação moldam e são moldados por processos no nível da comunidade. Este tipo de estudos tem indicado que a pesca pode modular fortemente as propriedades estruturais das redes tróficas, dispersando amplamente os efeitos através do sistema; e em termos da gestão e conservação, sugerem o foco nas espécies com propriedades estruturais únicas visando manter a integridade estrutural (Gaichas & Francis, 2008; Navia et al., 2016). De outro lado, tem sido realizados progressos significativos sobre como a pesca afeta a dinâmica, a persistência da diversidade marinha biológica e a sua própria sustentabilidade (Glaum et al., 2020; Ávila-Thieme et al., 2021), identificando efeitos indiretos positivos sobre espécies não capturadas (Ávila-Thieme et al., 2021), porém efeitos indiretos negativos para a sustentabilidade ecológica e económica ao longo prazo através da indução de cascatas de extinção (Glaum et al., 2020).

Durante as últimas décadas, os efeitos dos processos *bottom-up* (de baixo para cima) e *top-down* (de cima para baixo) acarretados por uma única espécie e que podem causar amplas mudanças em nível comunitário, permitiram o desenvolvimento de conceitos como espécies-chave (Paine, 1969), engenheiros de ecossistemas (Jones et al., 1994) e, mais recentemente, hubs de rede (Guimerà & Amaral, 2005; Olesen et al., 2007). Da mesma forma, podemos assumir que diferentes tipos de pesca devem atuar como *engenheiros de biodiversidade* com amplos impactos na estrutura e dinâmica ecológica e evolutiva das redes tróficas marinhas. Assim, esta abordagem proposta tem um grande potencial para melhorar a nossa capacidade de compreender, prever e gerenciar os impactos da pesca, tanto na escala artesanal como industrial (Maschner et al., 2009; Dunn et al., 2016; Pérez-Matus et al., 2017; Glaum et al., 2020; Ávila-Thieme et al., 2021) sobre a biodiversidade os serviços ecossistêmicos.

Objetivos da tese

O objetivo geral desta tese é fazer a ponte entre a abordagem de redes, a ecologia de comunidades marinhas e a desenho de estratégias de conservação fundamentadas teoricamente e com dados empíricos. Procuramos atingir tal objetivo através da utilização de uma base de dados abrangente que engloba dados de interações tróficas entre espécies marinhas em escala comunitária, da zona centro-sul da costa do Pacífico Colombiano, juntamente com informações sobre padrões de pesca regionais, para realizar análises estruturais e de modelagem de redes para avaliar os efeitos da pesca na estrutura e dinâmica da rede trófica. Ao fazê-lo, pretendemos elucidar os mecanismos que moldam a dinâmica da comunidade, que podem ser potencialmente úteis para fornecer conhecimentos inovadores para a regulamentação da pesca e para as políticas e práticas de conservação marinha.

Como primeiro passo para este objetivo geral, tivemos o objetivo específico de explorar e discutir como a ferramenta de redes é utilizada para compreender a arquitetura da biodiversidade marinha e para prever a resposta das redes tróficas às estratégias alternativas de gestão, tais como a redução da pressão da pesca sobre determinadas espécies-alvo, a fixação de quotas de captura de peixes, ou a remoção seletiva de determinadas espécies do sistema.

O segundo passo para o nosso objetivo geral, foi descrever a estrutura da rede trófica e identificar os papéis topológicos desempenhados pelas espécies nativas com categorias de conservação variáveis e com importância na pesca de pequena e grande escala. Subsequentemente, realizamos simulações estáticas de extinções de espécies e regulamentos de pesca (supressões de pescarias específicas) para avaliar suas potenciais consequências na estrutura da rede e na distribuição global dos papéis topológicos.

O terceiro passo para o nosso objetivo geral é desenvolver um modelo de rede adaptativa para organizar e formalizar vários pressupostos sobre a forma como as interações das espécies marinhas mudam ao longo do tempo, os quais sustentaram o modelo matemático em que a dinâmica das interações, as abundâncias e traços das espécies interagem entre si para reconfigurar as propriedades ecológicas das comunidades sob perturbações induzidas pela pesca. Espera-se que o modelo adaptativo da rede melhore a interface da nossa abordagem de rede e a concepção de estratégias de conservação, prevendo propriedades estruturais e dinâmicas emergentes, que fornecem parâmetros que podem ser estimados no campo.

Neste sentido, os modelos fornecem previsões testáveis que surgem de uma forma abrangente dos processos estruturantes que estão incorporados na estrutura do modelo – o qual é um papel chave, mas muitas vezes negligenciado dos modelos matemáticos em Ecologia e Evolução (Servedio et al., 2014).

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The use of ecological networks as tools for understanding and conserving marine biodiversity

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1 Introduction

The integrative understanding and management of anthropogenic and ecological processes that drive marine biodiversity are key to conserving marine ecosystems (Worm et al., 2006; Lotze et al., 2011; Dunne et al., 2016, Estes et al., 2016). A variety of anthropogenic pressures threaten marine biodiversity by changing patterns of species richness, ecological interactions and associated ecosystem functions at multiple spatial and temporal scales. Such pressures include overfishing (Jackson et al., 2001; McCauley et al., 2015; Pauly & Zeller 2016), pollution (Nixon 1995; Islam & Tanaka 2004), introductions of alien species (Bax et al., 2003; Vitousek et al., 1997), and climate change (Hoegh-Guldberg & Bruno 2010; Hillebrand et al., 2018). In addition, extinction of native species due to overfishing change patterns of species interactions, affecting community stability and threatening the long-term persistence of marine biodiversity (Jennings & Kaiser 1998; Lotze et al., 2011; Gilljam et al., 2015).

The urgent need of mitigating anthropogenic impacts on the biological diversity of oceans led to novel methodological approaches aimed to bridge theoretical Community Ecology and conservation strategies aimed to protect marine biodiversity. Knowledge of ecological and evolutionary processes that shape food webs -- which are networks defined by trophic interspecific interactions -- is the cornerstone of system-based conservation approaches aimed to ensure the long-term persistence of functionally diverse marine ecological communities (Dunne et al., 2002; Bascompte et al., 2005; Navia et al., 2012a). On the way to gaining insight into food web organization and its consequences for community dynamics and ecosystem functioning, numerous controversies have emerged among researchers, not so much as to whether humans drive deleterious effects on food webs, but rather about their magnitude and the levels of biological organization affected by such effects (Navia et al., 2012b). On one hand, intense fishing pressures over the past 50 years have arguably reshaped the most fundamental properties of marine food webs, including species richness, abundances, trait-values distributions and patterns of ecological interactions (Pauly et al., 1998; Jennings et al., 1999; Lotze et al., 2011; Dunne et al., 2016). On the other hand, ongoing anthropogenic changes may mostly affect species targeted by fisheries but do not necessarily imply community-level degradation (Essington et al., 2006; Litzow & Urban 2009). Despite such controversy, growing evidence supports that anthropogenic activities rapidly reshape patterns of feeding interactions at the whole-community (network) level and lead to the rewiring of marine food web architecture just a few years after commercial exploitation starts (Baum & Worm 2009; Ritchie & Johnson 2009). As anthropogenic changes in marine communities affect species abundances and trait diversity, they threaten the stability, functioning and persistence of marine ecosystems (Jennings & Kaiser 1998; Lotze et al., 2011; Gilljam et al., 2015).

In the last decades, the structural analysis of ecological networks has emerged as a powerful tool for fisheries management and conservation planning (Solé & Montoya 2001; Dunne et al., 2002; Stouffer & Bascompte 2010; Ortiz et al., 2015; Navia et al., 2016). Empirical knowledge on food web structure and theoretical works on how topological properties relate to network persistence have unraveled fundamental relationships between biodiversity structure and ecosystem functioning (Worm et al., 2006; Lotze et al., 2011; Estes et al., 2016, Yen et al., 2016). Network analyses also allow us to identify the topological role that each species plays within a food web, which can be used as a proxy for its contribution to community dynamics and hence inform conservation prioritization strategies (e.g., Luczkovich et al., 2003; Dunne et al., 2004; Bascompte et al., 2005; Jordán, 2009, Jordán et al., 2009; Rezende et al., 2009). Such advances in ecological network theory can greatly help us to understand, predict and manage the effects of anthropogenic impacts on marine biodiversity (Dunne et al., 2016).

Beyond structural analyses, dynamic network modeling using computer simulations can provide theoretically founded predictions on how biodiversity loss is expected to reshape community resilience and functional diversity, and hence influence the long-term persistence of ecosystems (Dunne et al., 2002; 2016; Raimundo et al., 2018a). Network models can greatly benefit from species-interaction data widely available for different types of ecosystems (e.g., Gaichas & Francis 2008; Navia et al., 2010, 2016, 2019; Bornatowsky et al., 2014, 2017; Marina et al., 2018; Endrédi et al., 2018). In addition to informing models of community dynamics, ecological network data can enhance strategies of environmental education, as they allow the visualization of ecological communities, a level of biological organization that is key for biodiversity maintenance but rarely addressed by education professionals outside specialist circles. By incepting the community ecology perspective into conservation and environmental education programs, the network approach can also greatly contribute to public engagement through communication, citizen science and evidence-based advocacy for decision-makers (Pocock et al., 2016).

In this chapter, we discuss network tools commonly used for understanding the architecture of marine biodiversity and for predicting how food webs are expected to respond to alternative management strategies, such as reducing fishing pressure on particular target species, setting fish catch quotas, or selectively removing particular species from the system.

2 Background

2.1 *Advances in network ecology and their relevance for Conservation*

The network approach to complex systems has been widely applied in Ecology, providing synthetic metrics to describe patterns of interspecific interactions that characterize community structure (Strogatz 2001; Montoya et al., 2006). Species-interaction networks capture the fundamental relationship between the architecture of biodiversity and ecosystem functions, whose understanding can improve our ability to predict how anthropogenic perturbations change biodiversity dynamics (Dunne et al., 2002; Jordano 2016). Empirical knowledge of ecological network structure (e.g., Pascual & Dunne 2006; Bascompte & Jordano 2014) associated to a diversity of structural analyses (e.g., Olesen et al., 2007) and network modeling approaches (e.g., Allesina & Tang 2015) are shedding light on mechanisms by which species interactions modulate ecological and evolutionary dynamics at the whole-community level (e.g., Thébault & Fontaine, 2010, Guimarães et al., 2017). The ecological network approach is feeding integration between ecological and evolutionary theories, based on methodological advances and an unprecedented availability of biodiversity big data; such epistemological and methodological innovations now support comprehensive predictive frameworks designed to formulate and test theoretically informed hypotheses on how human-induced effects change the most fundamental community properties, such as resilience and functional diversity (Raimundo et al., 2018a).

Several works have applied the network approach to unravel the impacts of anthropogenic effects -- such as fishing or hunting -- on biodiversity, particularly regarding the consequences of species extinctions (Gaichas & Francis 2008; Navia et al., 2010, 2016; Dunne et al., 2016; Pérez-Matus et al., 2017). Network modeling allow us to predict how species extinctions and other anthropogenic effects will affect ecological and evolutionary dynamics shaping food web structure affecting ecosystem functions (Ings et al., 2009; Thébault & Fontaine 2010; Rohr & Bascompte 2014; Yen et al., 2016; Raimundo et al., 2018b). Complementarily, structural analyses of ecological networks allow us to understand how patterns of interactions modulate demographic and evolutionary processes within communities, and how such dynamics change species-level properties, such as traits and abundances (Poisot et al., 2015). Structural analyses can also unravel topological roles that species play within networks, which inform how they influence the propagation of ecological and evolutionary effects (e.g., Olesen et al., 2007). Understanding and predicting how species interaction networks are assembled and respond to anthropogenic disturbance is pivotal for the design of process-based strategies aimed to restore and conserve biodiversity and ecosystem functions at the community level (Raimundo et al., 2018a).

2.2 Macroscopic and microscopic patterns in marine food webs: from network structure to species topological roles

Similar to species-rich terrestrial communities governed by joint demographic effects of multiple species interactions (Raimundo et al., 2018b), the structure and dynamics of marine food webs can be described and understood in terms of their topological patterns (Dunne et al., 2004). A growing body of evidence arising from structural analyses of trophic networks (e.g., Navia et al., 2012a; Barabási 2016; Lau et al., 2017) supports that structural attributes are recurrent over different ecoregions. The major motivation to study macroscopic structure of ecological networks is that understanding how network architecture modulates the propagation of effects at the system level is key for the development of functional conservation strategies based on ecological and evolutionary processes that shape community structure and dynamics. Architectural patterns that are recurrent in ecological networks, such as modularity (Olesen et al., 2007; Rezende et al., 2009) and nestedness (Bascompte & Jordano 2014; Cantor et al., 2017), have been related to the stability of networks and the extent to which they can persist facing several types of environmental stressors (Solé & Montoya 2001; Dunn et al., 2004; Bascompte et al., 2005; Thébault & Fontaine 2010).

Structural analysis of marine food webs can also inform the roles that each species plays within an ecological community (Guimerà & Amaral 2005; Jordán et al., 2006; Olesen et al., 2007). Topological metrics that describe species-level properties within networks include species connectivity (Degree) and other indexes that inform species topological roles, for instance, regarding their centrality within network paths (Betweenness, Closeness) or their contribution to network cohesion (Network hubs, Keystone index; Topological uniqueness) (Jordán et al., 1999; 2006; Jordán 2001; 2009; McMahon et al., 2001; Krause et al., 2003; Guimerà & Amaral 2005). Understanding species topological roles enlightens how network properties emerge dynamically in the course of network evolution (Gaichas & Francis 2008; Bornatowski et al., 2017). Theoretical and empirical research suggest that topological roles are driven by traits that mediate ecological interactions, such as niche breadth, individual motility, and trophic positions, alongside with community-specific properties that constrain patterns of interaction and species potential for interaction rewiring, such as phylogenetic clustering (Rezende et al., 2009, Guimerà et al., 2010; Borthagaray et al., 2014, Olmo-Gilabert et al., 2019).

Species topological roles represent a proxy for species contribution to community structure, which arguably can be extended to its dynamics. Importantly, we shall notice that topological roles are not static but change over time due to a variety of mechanisms driving species connectivity, which include temporal species turnover (Díaz-Castelazo et al., 2013) and several adaptive mechanisms of interaction rewiring (Valdovinos et al., 2010; Raimundo et al., 2018a). From an applied perspective, combining knowledge of macroscopic (global) network patterns and microscopic (local) information, such as provided by topological role analyses, can sustain testable predictions about system-level consequences of ongoing anthropogenic impacts affecting marine biodiversity (Dambacher et al., 2010; Navia et al., 2010, 2016, 2019; Bornatowski et al., 2014; Dunne et al., 2016).

Analyses of species topological roles represent the cornerstone for the development of innovative community-level conservation strategies because they allow the identification of species whose connectivity patterns lead to strong effects on intertwined demographic dynamics at the community level and, in addition, also represent key connections for the flow of matter and energy at the ecosystem level. For example, a few fish species, such as Gadus macrocephalus (Pacific cod) and *Hippoglossus stenolepis* (Pacific halibut), are structural connections that define the food web backbone in the Gulf of Alaska (Gaichas & Francis 2008). In Brazil, large shark predators at higher trophic levels exert top-down effects that drive the ecological dynamics of species within lower trophic levels (Bornatowski et al., 2014). Species playing key topological roles are often those most connected, such as network hubs defining the backbone of modular networks that have many intra- and inter-modular links (Olesen et al., 2007). On the other hand, among-module synchronization in modular networks that miss network hubs will depend on connector species that link modules but are not necessarily highly connected (Guimerà & Amaral 2005; Olesen et al., 2007). Additionally, under particular network architectures, such as small-world patterns and scale-free properties, species centrality does not correlate with structural patterns (Navia et al., 2010, 2016).

Marine food webs show recurrent topological patterns, such as small-world structures (Watts & Strogatz 1998; Marina et al., 2018) and modularity (Newman & Girvan 2004). Modularity has been reported for Arctic (Kortsch et al., 2015), Antarctic (Saravia et al., 2018), temperate (Krause et al., 2003; Pérez-Matus et al., 2017) and tropical marine food webs (Rezende et al., 2009). Theory predicts that modularity will increase the stability in food webs (May 1972, 1973; Pimm 1979; Thébault & Fontaine 2010; Stouffer & Bascompte 2011) by preventing the spread of perturbations, i.e., modular structures would constrain the impact of disturbances either because the perturbations remain within a single compartment or reach other compartments with decreased magnitudes (Krause et al., 2003). On the other hand, it has also been argued that under certain conditions, modularity can increase the likelihood of species extinctions and co-extinctions (Dáttilo 2012) as deleterious effects remain within a module and will eventually be amplified by mechanisms such as feedback loops or extinction cascades. Despite its recurrent role as a major driver of marine biodiversity, a comprehensive overview of the applied consequences of modularity in marine food webs is mostly lacking.

2.3 Processes shaping the structure of marine food webs

Several non-mutually exclusive mechanisms have been proposed to explain food web patterns. A first type of mechanisms refers to processes involving phenotypic traits that mediate ecological interactions (Cohen et al., 1993; Laigle et al., 2018), which are phylogenetically constrained (Webb et al., 2002; Cattin et al., 2004; Rezende et al., 2009). A second class of mechanisms driving food web architecture encompasses neutral processes arising from spatio-temporal variation in abundance distributions, which determine the likelihood of pairwise species interactions based on encounter probabilities (Cohen et al., 2003; Vásquez et al., 2007). Although the relative roles played by trait-based and neutral processes in shaping interaction networks vary over different biological systems, both contribute to network dynamics to some extent. Reciprocal effects between trait-based and neutral processes form feedback loops that connect ecological and evolutionary processes at the community level. Such feedback loops define eco-evolutionary dynamics that shape interaction patterns, abundance distributions and trait diversity (see Raimundo et al., 2018a and references therein).

We are still in the first steps regarding the application of eco-evolutionary theory to the management of biodiversity and ecosystem functions. Bridging knowledge on trait-interaction-abundance feedbacks that shape ecological network dynamics (Poisot et al., 2015) and the design of conservation strategies is key to ensure the much-needed inception of evolutionary community ecology into governance and policymaking (Jørgensen et al., 2019). Facing such a challenge, we shall consider that abundances and traits can vary widely over space and time and, in addition, are influenced by processes at different levels of biological organization: from genes to individuals, populations, communities, and ecosystems (Pacheco et al., 2006). In order to integrate several classes of structuring processes into robust predictive frameworks accounting for the dynamics of marine biodiversity, we can rely on dynamic network models that have been increasingly applied to investigate the interplay among ecological and evolutionary processes that account for community properties (e.g., Zhang et al., 2011; Suweis et al. 2013; Poisot et al., 2015).

2.4 The roles that fisheries play within food webs

The development of dynamic network models that can enlighten fishing and conservation policies requires a proper consideration of the interplay between anthropogenic and eco-evolutionary processes shaping contemporary marine biodiversity. Human-induced changes in marine ecosystems have occurred for centuries but only in the past decades their impacts reached a global scale (Jackson et al., 2001; Lotze et al., 2011; McCauley, et al., 2015). There are three major anthropogenic effects that affect marine biodiversity and ecosystem functioning, namely: 1) changes in nutrient cycles and climate, which affect bottom-up ecosystem processes, 2) fishing activities, which impose top-down effects threatening species diversity, and 3) habitat degradation and contamination, which affect processes across all trophic levels (Navia et al., 2012a). Since fisheries impose both direct and indirect effects on marine ecosystems, fishing impacts on target and non-target fish species are likely to propagate within the food web and emerge as changes in ecological properties at the community level (Standstöm et al., 2005).

To date, most studies have focused on the effects of fishing on population dynamics, most often of charismatic species or of taxa with higher commercial values (e.g., Lotze & Worm 2009; Lotze et al., 2011). Although some works have assessed effects of anthropogenic activities on functional groups or entire food webs (e.g., Jackson et al., 2001; Pandolfi et al., 2003), the consequences of human impacts on the structure and functioning of marine ecosystems remain mostly unclear (Lotze et al., 2011). On the one hand, several studies found that fisheries reshape patterns of species interactions whose effects propagate at the community level and change the distributions of species abundances (Myers et al., 1996) and of traits that mediate ecological interactions (Jennings et al., 1999; Bianchi et al., 2000), which, in turn, trigger further changes in network organization and dynamics (Myers et al., 2007; Barraclough, 2015; Poisot et al., 2015; Raimundo et al., 2018a). Therefore, it can be generally expected that the consequences of fishery-induced extinctions will reshape network architecture (Dunne et al., 2016; Pérez-Matus et al., 2017), community composition

(Hutchings & Baum 2005), and trophic structure (Pauly et al., 1998; Ferretti et al., 2010), such as have been reported for temperate (Shepherd & Myers 2005; Myers et al., 2007; Gaichas & Francis 2008; Coll et al., 2009) and tropical marine ecosystems (Stevens et al., 2000; Navia & Mejía-Falla 2016).

Fisheries often act as adaptive foragers within ecosystems by optimizing capture rates (Begossi 1992; Bertrand et al., 2007; Poos & Rijnsdorp 2007) and by switching target species to minimize costs and maximize profits (Acheson 1988; Sethi et al., 2010). Such dynamic fishing patterns are expected to trigger eco-evolutionary feedbacks that will propagate over the whole community and reshape abundance and trait distributions (Barraclough 2015, Tromeur & Loeuille 2018). The consequences of adaptive foraging by fisheries at the ecosystem level remains unclear. Adaptive harvesting can arguably stabilize marine ecological communities by continuously reallocating fishing pressures to target more abundant prey species, thereby counterbalancing negative effects of fishing on rare species, releasing them from interspecific competition and hence contributing to community stability and diversity (Kondoh 2003; Loeuille 2010). On the other hand, adaptive interaction switches performed by fisheries could induce abrupt phase shifts with unexpected consequences for community structure and dynamic (Jackson et al., 2001; Estes et al., 2011, 2016; Conversi et al., 2015). To shed light on such contradictory predictions regarding the network-level consequences of fishing impacts, fisheries can be incorporated into food web analyses as additional nodes that are analogous to high-level predators. Incorporating fisheries as dynamic agents within the food webs, whose interaction patterns shape and are shaped by community-level processes, can greatly improve our ability to understand, predict and manage fishing impacts (Maschner et al., 2009; Dunn et al., 2016; Pérez-Matus et al., 2017). It is widely acknowledged by ecologists that several types of bottom-up and top-down effects imposed by single keystone species can lead to broad changes at the community level (Paine 1969; Jones et al., 1994). Similarly, fisheries are likely to act as network hubs (Guimerà & Amaral 2005; Olesen et al., 2007) and hence drive marine food web structure and dynamics.

3 Analytical approaches

Topological changes in food webs arise as a consequence of the adaptive rewiring of multi-species interactions due to a variety of ecological and evolutionary mechanisms (see Raimundo et al. 2018a). Understanding the extent to which such structural changes in trophic networks affect ecosystem dynamics and stability is a key issue for biodiversity conservation (Pimm 2002; De Ruiter et al., 2005). The perception that community- and ecosystem-level approaches are much-needed to conserve biodiversity led to integrative conceptual frameworks, such as the multispecific management (May et al., 1979; Yodzis 2000) and ecosystem approaches (Grant et al., 1997), which recognize the need to take into account not only functional roles played by single species but consider responses of whole species assemblages to more accurately model food web dynamics (Jordán et al., 2006). Although changes in species composition can be used as a proxy for ecosystem perturbations, a systemic approach capable of providing comprehensive indicators of changes in structural and functional properties of ecological communities depends on the description of species-interaction networks, which account to the ecological and evolutionary processes driving biodiversity dynamics at the community level (Dunne et al., 2002; Bascompte et al., 2005).

Natural trophic networks show recurrent structural properties across ecosystems, which provide benchmarks for the evaluation of biodiversity erosion within degraded ecosystems subject to intense human activities (Dell et al., 2005). Network analyses provide several tools that can connect theoretical foundations and methodological tools provided by quantitative community ecology to food web conservation and management. In what follows, we summarize analytical approaches commonly used to describe food web properties and discuss their current and potential interface with marine biodiversity conservation and management.

3.1 Structural Analysis: local and mesoscale indices

Several local and mesoscale network indices, most of which consider distances between nodes (Wasserman & Faust 1994), are widely applied to describe network- or species-level properties within marine food webs. Such indices take into account every possible (direct and indirect) interaction between species i and j. Regarding local indices, the most fundamental metric describing a species (node) is its degree (D), which is computed as the number of direct links to other species (nodes) for both prey (in-degree) and predators (out-degree) (Jordán et al., 2006). If the degrees of all nodes within the network are known, one can describe the distribution of links, i.e., the statistical distribution of degree-values that can readily inform key network-level properties. For example, if the degree distribution follows a power law, the network is said to be scale-free (Solé & Montoya 2001; Dunne et al., 2002; Montoya & Solé 2002).

Several topological indices are built on information about node neighborhood and interaction paths between neighbours, such as a family of well-known metrics named “Centrality indices”. For example, betweenness centrality (BC) measures how a node is incident to many shortest paths in the network. If a trophic group i has a high BCi value, then removing this group from the network decreases the overall degree of network synchronization, as interaction paths accounting for rapidly spreading effects will no longer be available (Jordán et al., 2006). Closeness centrality (CC) is another widely used metric from this family of indices, which quantifies the length of minimal paths from any given node to all others (Wassermann & Faust 1994). Removing trophic groups characterized by high CCi will have repercussions on most other groups within the network (Jordán et al., 2006).

Given the structural complexity of species-rich interaction networks, the graphic representation of indices such as those described above is an important tool to assist the interpretation of the results, especially when the aim is to communicate findings to non-scientific audiences or decision-makers (Pocock et al., 2016). As an example, we present graphs resulting from centrality analyses of a binary matrix (Navia 2013, Fig. 1a) depicting predator-prey interactions at the Gulf of Tortugas, Colombian Pacific coast. First, we plotted the overall network structure by showing undirected interactions between predators and prey (Fig. 1b). Subsequently, we computed degree (D), betweenness centrality (BC), and closeness centrality (CC) to gain insight into key local and global network properties. In figure 1c, node sizes are proportional to their degrees and hence it is possible to identify the most connected species (nodes), such as shrimps (green nodes), sharks (gray nodes), and rays (black nodes). Based on betweenness centrality (BC), we detected that some species of bony fishes (red nodes), sharks and rays (black and gray nodes), and shrimps (green nodes) are likely to drive the propagation of ecological and evolutionary effects within the network (Fig. 1d). Finally, closeness centrality (CC, smaller nodes correspond to higher closeness values) informs that predators, such as sharks and rays, alongside with the most consumed prey, such as shrimp and squids, are key drivers of effect propagation within the food web (Fig. 1e). These examples illustrate how the structural analyses of ecological networks can rapidly provide information for fishing management measures, which in this case should focus on shrimp, sharks and rays that are key drivers of network dynamics. Comprehensive information on the above-mentioned indices and their application to marine environments are provided by Wassermann & Faust (1994), Jordán et al. (2006), Abarca-Arenas et al. (2007), Dambacher et al. (2010), Navia et al. (2010, 2016, 2019), Oshima & Leaf (2018).

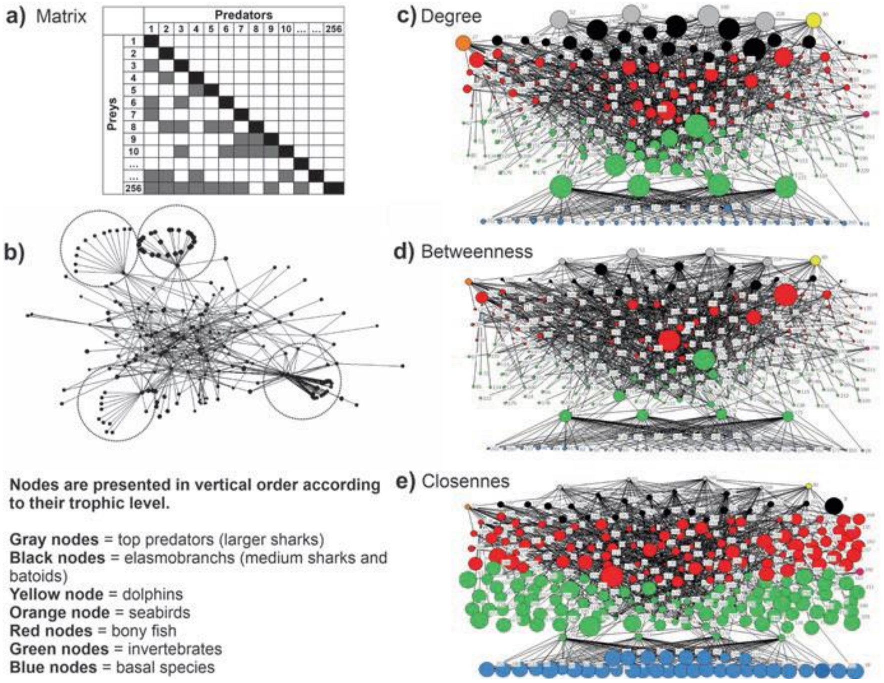


Fig. 1 Visualization of degrees and centrality indices of food web of the Gulf of Tortugas, Colombian Pacific coast (Figures c, d, e are modified from Navia, 2013)

3.2 Keystone species and Keystone Species Complexes

Many of the indexes mentioned so far consider interactions between neighbouring nodes, but not necessarily whole systems (Benedek et al., 2007). Species can be in pivotal topological positions within ecological networks, exerting disproportionately strong structural and functional effects at the community level (Capocefalo et al., 2018). The propagation of secondary effects (e.g., trophic cascades or apparent competition; Menge 1995) within food webs are hard to predict without high-quality information on network structure. Fortunately, the increasing availability of species-interaction big data now provides unprecedented conditions for ecologists to apply structural network analysis in order to identify species that play key topological roles and properly sustain system-level biodiversity conservation strategies (Capocefalo et al., 2018, Raimundo et al., 2018a).

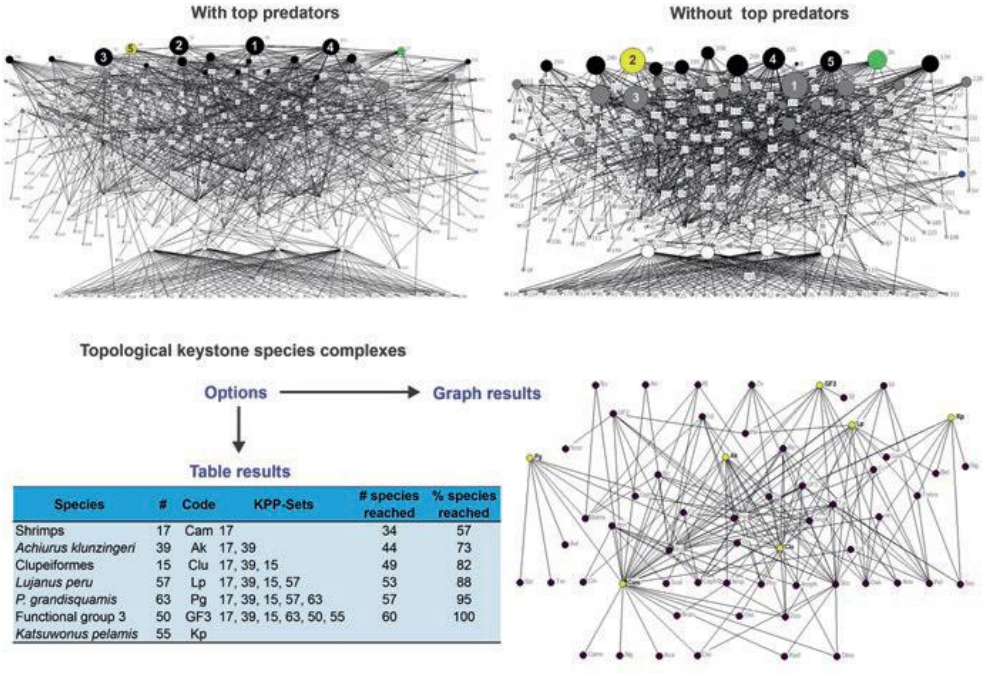
The use of quantitative species-interaction data to detect those taxa that act as key network nodes (defined as topological keystone species, Jordán et al., 1999, 2006; Libralato et al., 2006) can greatly improve system-level conservation strategies because the extinction of such species will cause stronger effects at the network level (Jordán & Scheruring 2002; Jordán et al., 2003; Allesina et al., 2006). Based on the "net status" of species (Harary, 1961), Jordán et al. (1999, 2006) proposed the Keystone index as a straightforward procedure to identify species that, due to their topological position within the network of interspecific interactions, are expected to drive community dynamics.

The keystone index informs the number of direct connections among neighboring species (nodes) and how such species are interconnected (Jordán et al., 2006), emphasizing vertical interactions over horizontal ones (e.g., trophic cascades vs. apparent competition). In addition, it also characterizes a species' positional importance by distinguishing direct from indirect effects, as well as bottom-up from top-down effects (Jordán 2001).

Mesoscale indices have been favored over other more local indices, such as the distribution of trophic connections (Montoya & Solé 2002; Dunne et al., 2002), or more global ones, such as food web connectance (Martinez 1992). The latter, for example, reflects the global connectivity of the network but does not provide information on the topological position of individual nodes or indirect interaction pathways and, therefore, does not allow inferences on indirect effects, such as apparent competition and trophic cascades (Holt & Lawton 1994; Menge 1995).

Overall, mesoscale indices are recommended when the purpose of the study is to unravel relationships within a community (Jordán & Scheuring 2002) and, especially, when we aim to quantify the relative importance of a given species within a community (Jordán et al., 2006). In this sense, Jordán (2009) presented the concept of 'trophic field overlap', which refers to the positional uniqueness of species. The corresponding overlap metric quantifies species topological redundancy within interaction networks and hence identifies species showing rich, as well as unique interaction patterns (Jordán 1999). Using the indices of topological importance and redundancy, Navia et al. (2016) found that ecosystem-based fisheries management should prioritize not only highly-central species (e.g., shrimps, which are species of high commercial value in the area, white nodes 170, 171, 173 and 174, Fig. 2) but should also consider species with unique structural properties such as sharks with low topological redundancy (black nodes with numbers 1 until 4; Fig. 2). The topological keystone index (KI) and topological uniqueness (TU) can also be graphed to facilitate the interpretation of the results (Fig. 2). In this example, the values of TU with and without top predators depict the structural effect that the loss of these species would have on the network and how the topological redundancy would be affected. When the extinction of top predators (large sharks) is simulated, the lower values of topological redundancy are transferred to bony fishes (gray nodes 1 and 3), marine mammals (yellow node) and to medium-sized shark and ray species, implying the reorganization of the top-down structure of the network.

Nevertheless, beyond using information on the positional importance of single nodes within networks, the development of system-level conservation strategies can benefit from analyses that inform (i) the topological roles of whole sets of species (nodes) or, complementarily, (ii) exactly which set of nodes is the most important in maintaining network integrity (by quantifying the structural effect of its deletion). Network analyses considering multi-species sets are founded on both empirical knowledge and modeling (Daily et al., 1993; Ortiz et al., 2013, 2015, 2017), which together allow the identification of keystone species complexes that should be prioritized in conservation strategies (Daily et al., 1993). Indeed, current studies in landscape ecology (Pereira & Jordán 2017; Pereira et al., 2017) reinforce the notion that the positional importance of species within food webs should be characterized simultaneously rather than independently in order to make system-level conservation strategies more effective.



Species	#	Code	KPP-Sets	# species reached	% species reached
Shrimps	17	Cam	17	34	57
Achiurus klunzingeri	39	Ak	17, 39	44	73
Clupeiformes	15	Clu	17, 39, 15	49	82
Lujanus peru	57	Lp	17, 39, 15, 57	53	88
P. grandisquamis	63	Pg	17, 39, 15, 57, 63	57	95
Functional group 3	50	GF3	17, 39, 15, 63, 50, 55	60	100
Katsuwonus pelamis	55	Kp			

Fig. 2 Visualization of topological uniqueness (TU) with and without top predators and options to show results of the Key Player Problem (table or figure). See the text for methodological details. (Figure with top predators taken and modified from Navia et al., 2016)

Despite the potential of analyzing keystone species complexes as a tool to guide the design of marine biodiversity conservation strategies, few works have successfully addressed this issue. A promising example is the application of the concept of key species groups (Daily et al., 1993) to solve the KeyPlayer (KP) problem (Borgatti 2003a) in the context of food webs. According to the proposal of Benedeck et al. (2007) and Ortiz et al. (2013), based on quantitative or semi-quantitative models (mass-balance and Loop Analysis), keystone species complexes (KSCs) consist of an interaction core formed by species and/or functional groups linked by strong interspecific interactions. The next step is to identify which KSCs maximize network integrity according to two criteria. First, "Fragmentation" (KPP-1) is computed as the contribution of each of node to network cohesion and informs the identity of nodes whose removal will maximize network fragmentation. The second criteria, "Expansion" (KPP-2), identifies which KSCs maximize the fast propagation of effects over the whole network. This analysis can be performed using the Key Player 1.1 routine (Borgatti 2003b). For instance, applying the KPP-2 criterion to a tropical food web in the Colombian Pacific coast without top predators (Navia unpub. data) shows that six species (KPP-2 sets) -- including mostly species of medium trophic levels (yellow nodes in Fig. 2) -- are required to ensure the propagation of ecological effects to 100% of the food web.

3.3 Modularity

Modularity is a pervasive structural property in marine food webs, which occurs when a subset of species interacts more frequently among themselves than with the other species in the network (Krause et al., 2003; Newman & Girvan 2004; Stouffer & Bascompte 2011). Modular food webs have been reported for Arctic (Kortsch et al., 2015), Antarctic (Saravia et al., 2018), temperate (Krause et al., 2003; Pérez-Matus et al., 2017) and tropical ecosystems (Rezende et al., 2009). However, the ecological and evolutionary dynamic implications of modularity are not a consensus. Theory predicts that modularity will increase food web stability (May 1972, 1973; Pimm 1979; Thébault & Fontaine 2010; Stouffer & Bascompte 2011) by preventing the spread of perturbations, since disturbances will be likely to remain within a single compartment or reach other compartments with decreased magnitudes (Krause et al., 2003).

For modular food webs, the topological roles that species play result from the balance between their connectivity between and within modules (Guimerà & Amaral 2005; Saravia et al., 2018). Such a balance implies four categories of topological roles: (i) network hubs, which are species showing high degrees of both intra- and intermodular connectivity, i.e., these species form the network backbone and hence their removal are expected to have broad structural and dynamical consequences; (ii) module hubs, which are species that show low intermodular connectivity but high intramodular connectivity, i.e., these species drive local dynamics; (iii) connectors, which are species showing high intermodular connectivity but low intramodular connectivity, i.e., these species do not belong to modules but can be unique connections between large modules, even if they have a low number of connections; (iv) peripherals, which are species with low intra and intermodular connectivity and hence expected to have minimal impacts on community dynamics (Guimerà & Amaral 2005; Olesen et al., 2007).

A preliminary analysis of topological roles in a modular tropical marine food web (Fig. 3; Márquez-Velásquez et al., unpub data) shows that a small subset of species acting as network hubs (2% of the species pool) and module hubs (4% of the species pool) account for the network backbone. Among these, three shark species acts as network hubs, suggesting that top-down effects drive food web dynamics. Shrimp species, some bony fish species as Pacific snappers and catfishes, and a stingray act as module hubs and hence also are pivotal elements sustaining network compartmentalization. Up to 85% of the species pool is formed by peripheral species, which are only locally connected. Species playing different topological roles are dispersed over all food web modules, which might suggest that species in the same module share functional traits, such as body mass (Laigle et al., 2018). These results support that multi-species management should go beyond protecting top predators and include at least module hubs and connectors to ensure the long-term persistence of community structure.

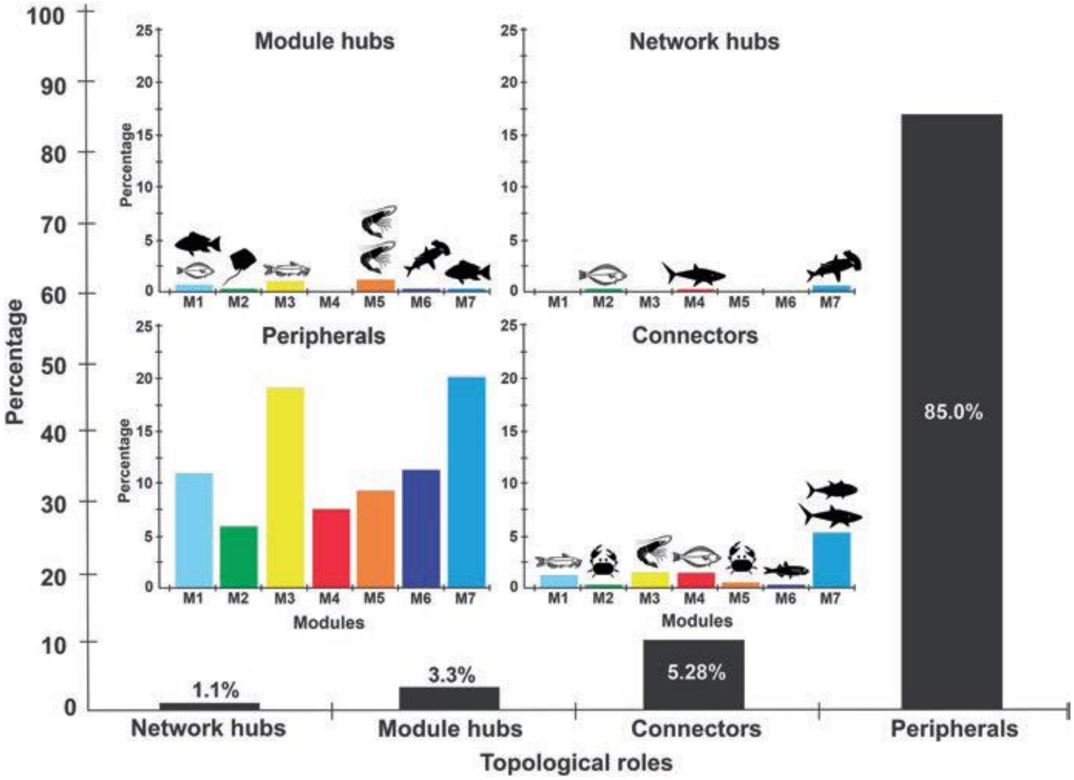


Fig. 3 Illustrative modular structure and topological roles of a tropical marine food web (Márquez-Velásquez et al., unpub data)

3.4. Linking network theory and modelling: An adaptive network models approach

Over the last two decades, empirical knowledge on ecological network structure (e.g., Pascual & Dunne 2006, Rezende et al., 2009) associated to the development of a diversity of structural analyses (e.g., Newman & Girvan 2004; Marina et al., 2018) and network modeling approaches (e.g., Gross & Blasius 2008; Allesina & Tang 2015) have set exceptional conditions for the design of novel approaches linking theoretical and applied Ecology and aimed to improve our understanding of how species interactions modulate ecological and evolutionary dynamics at the whole-community level (e.g., Thébault & Fontaine 2010).

Dynamic network modeling combined with computer simulations can provide theoretically founded predictions of how biodiversity loss is expected to reshape community-level properties, such as resilience and functional diversity, and influence the long-term persistence of ecosystems (e.g., Thébault & Fontaine 2010; Yen et al., 2016; Vinagre et al., 2019). Particularly, adaptive networks are a promising conceptual and modeling framework (Gross & Blasius 2008; Gross & Sayama 2009) that can help us to address trait-interaction-abundance feedbacks (Poisot et al., 2015) and deepen our understanding of eco-evolutionary mechanisms driving long-term community dynamics. An adaptive network is defined by the feedback loop between network structure and the properties of the nodes, i.e., it encompasses the mutual effects between changes in interaction patterns and associated network properties that characterize community structure and dynamics, such as modularity, and stability; and population-level, eco-evolutionary processes shaping the properties of species that form the network, such as their abundances and trait values (Gross & Blasius 2008; Gross & Sayama 2009).

Dynamic network models incorporating adaptive rewiring of interactions can help us to predict, for example, how improved fisheries regulations may promote competition releases and change the interaction patterns of natural network hubs, which may have broader structural consequences for network structure and ecological dynamics (Valdovinos et al., 2010; Márquez-Velásquez in prep., 2019). This integrative framework can shed light on the relationship between ecological network structure and ecosystem stability (Allesina & Tang 2015) by allowing the systematic investigation of how multiple structural alternatives may fulfill the conditions for species coexistence and network stability (Rohr et al., 2014).

Ultimately, adaptive networks can represent an integrative framework connecting theoretical and empirical research on community dynamics and promoting the design of experiments that can test key hypotheses to improve conservation and restoration strategies (Raimundo et al., 2018a).

4 Concluding remarks

Regardless of the approach used, food web studies rely on the availability of high-quality species-interaction data sustaining structural analysis and modeling. Natural history knowledge describing species diet and feeding ecology at the finest level of detail is mandatory, since it enables nuanced modelling of important ecological effects such as temporal, spatial, and sex and size-specific diet shifts. Depending on the approach applied, population-level information should be provided for model parameterization, such as production (i.e. biomass), productivity (i.e. mortality rates), abundances, and data on catches and discards.

Network analyses and models are much-needed tools to study difficult-to-delineate ecosystems, such as the oceans, where populations often cannot be manipulated and hence inferences on the relationship between species loss and community stability are not easy to obtain using empirical approaches. The network ecologist toolbox can partially reproduce marine ecosystems complexity and perform "computer experiments" that simulate community dynamics under several perturbation scenarios and conservation strategies. Predictions provided by network models can provide system-level information on biodiversity and ecosystem functions to decision-makers, which would otherwise be very difficult to obtain. On the other hand, modelers should not neglect the need of empirically testing their assumptions and predictions to avoid indiscriminate errors of extrapolation or overreaching conclusions.

Advances in ecological network modelling can allow us to understand and predict natural and anthropogenic impacts on marine biodiversity and the consequences of species extinctions. Therefore, understanding how interaction among marine species are assembled and respond to anthropogenic disturbance is pivotal for the design of process-based strategies aimed to conserve marine biodiversity at the community level. Species topological roles are not static but change over time due to a variety of mechanisms driving species connectivity, including temporal species turnover (Díaz-Castelazo et al., 2013) and adaptive mechanisms of interaction rewiring (Raimundo et al., 2018a). The next step to improve the application of the network approach to understand and manage marine biodiversity and ecosystem functions is to investigate topological roles of species change under anthropogenic pressures and its dynamic impacts on the systems.

A broad challenge that we shall face in order to advance the network approach to understand and manage marine biodiversity is to bridge dynamic network modeling, species-interaction big data, and biomonitoring approaches by using parameters that can be easily estimated in the field by conservation practitioners. Facing such a challenge, we can benefit from ongoing theoretical synthesis in Ecology and Evolution and a variety of novel methods for network analyses and modeling. This exciting perspective may allow us to combine theoretical and empirical Community Ecology to shed light on the processes driving ecological networks and improve our ability to manage marine biodiversity and ecosystem functions.

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CAPÍTULO II

Capítulo aceito para publicação no *ICES Journal of Marine Science.*

Resource partitioning between fisheries and endangered sharks in a tropical marine food web

Running title: Resource partitioning between fisheries and sharks

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Fisheries can act as top predators and affect marine biodiversity and ecosystem functioning via their target species. We studied a coastal food web in the Pacific Ocean that is modular and encompasses 360 species and small- and large-scale fisheries. Small-scale fisheries, two hammerhead sharks, one stingray, and one flatfish species are network hubs, interacting with multiple species among and within trophic levels and modules. Small-scale fisheries and endangered hammerhead sharks act as hyper-hubs, which are network hubs preying on other network hubs and likely imposing widespread top-down effects. Hyper-hubs have two consequences to network structure. First, they show low dietary overlap, connecting the network in complementary ways. Second, they have overlapping indirect interactions, suggesting they can strongly affect each other. Simulations assuming distinct fishery regulations and species extinctions of different trophic levels and topological roles did not change network structure but redefined hub identity. We hypothesize that competition shapes resource partitioning between fisheries and hammerhead sharks. Our findings suggest that ecosystem-level strategies informed by network approaches can optimize investments to conserve marine ecosystems and ensure food security over coastal areas in the developing world.

Keywords: artisanal fisheries, evidence-based conservation, industrial fisheries, the ghost of competition past.

INTRODUCTION

Human activities are fundamental processes currently shaping biodiversity patterns and ecosystem functioning over the Earth (Young *et al.*, 2016). Anthropogenic changes threaten ecosystems, urging us to develop evidence-based approaches to reconcile economic activities, social welfare, and biodiversity conservation (Worm *et al.*, 2009; Lotze *et al.*, 2011). Marine food production is one essential ecosystem service threatened by anthropogenic changes (Costanza *et al.*, 1997). Anthropogenic changes threatening marine ecosystems and food production include pollution (Nixon, 1995), alien species (Bax *et al.*, 2003), climate change (Hillebrand *et al.*, 2018), and overfishing (Pauly and Zeller, 2016). Specifically, overfishing is a severe threat to food provision, jeopardizing human populations that depend on fishing (FAO, 2020).

Overfishing has widespread effects on marine biodiversity, from the fitness of individuals (Pinsky and Palumbi, 2014) to the distribution of abundances and body sizes within populations (Pauly *et al.*, 1998; Baum and Worm, 2009) and patterns of species interaction (Gaichas and Francis, 2008; Navia *et al.*, 2012). Ecological networks describe patterns of species interactions at different spatio-temporal scales (Guimarães, 2020). At the ecosystem level, networks bridge our understanding of community structure and dynamics (Jordano, 2016), for example, by quantifying the species roles in community structure (Guimarães, 2020). In this sense, a recurrent structural pattern shown by ecological networks is modularity, in which groups of species interact more frequently among themselves than with other species within the network (Stouffer and Bascompte, 2011).

Distinct mechanisms, such as adaptive processes shaping ecological traits or interspecific variation in habitat specialization, can lead to modular food webs (Krause *et al.*, 2003; Rezende *et al*., 2009). Theory predicts that modularity enhances food web stability (May, 1973; Stouffer and Bascompte, 2011) by minimizing perturbation spreading (Krause *et al*., 2003). Empirical data show that modularity can sustain the long-term persistence of food webs even under intense environmental and fishing pressures (D'Alelio *et al*., 2019). Understanding how modularity enhances biodiversity persistence depends on quantifying species roles in the network structure. For example, lower incidences of highly connected species (network hubs) and other species whose interactions connect modules reduce the number of pathways that otherwise would allow cascading effects across the food web (Myers *et al*., 2007).

Networks allow in-depth assessments of the ecological consequences of fishing via direct and indirect effects (Bieg *et al*., 2018). Thus, network approaches complement other approaches that address fishing impacts on community properties (Worm *et al*., 2009; Lotze *et al*., 2011). For instance, the incorporation of fisheries as nodes within food webs provides insights into their impacts on marine communities (Dunne *et al.*, 2016; Pérez-Matus *et al*., 2017; Glaum *et al*., 2020; Ávila-Thieme *et al*., 2021). Such studies address, for example, how the decline of top predators triggers trophic cascades (Estes *et al*., 1998; Bascompte *et al.*, 2005); the spread of fishing effects via short interaction chains and small sets of target species (Gaichas and Francis, 2008; Navia *et al*., 2016); the impacts of fisheries as super-generalist consumers (Dunne *et al.*, 2016; Pérez-Matus *et al*., 2017), which can be positive for some non-target species (Ávila-Thieme *et al*., 2021) but often impose adverse outcomes for biodiversity persistence and fisheries (Glaum *et al.*, 2020).

One next step to improve evidence-based conservation strategies is to use the socio-ecological perspective on food web dynamics to study the interplay between marine species and fisheries in shaping ecological networks (Márquez-Velázquez *et al*., 2020). For example, it is relevant to assess whether interaction patterns of fisheries and top and mesopredators are redundant or complementary (Yodzis, 2001; Pichegru *et al*., 2009). Large sharks play central roles within marine food webs (Navia *et al*., 2010; Bornatowski *et al*., 2014). Describing shark dietary overlap with fishing targets can unravel mechanisms shaping their contemporary patterns of resource use and inform conservation strategies for these endangered species (Dulvy *et al*., 2014).

Ecological theory posits interspecific competition is a fundamental mechanism underlying patterns of ecological interactions (MacArthur and Levins, 1967; Connell, 1980). Prey abundance can often be a limiting factor leading to intense competition among marine predators (Ward *et al*., 2006; Hayata *et al*., 2021). Consequently, contemporary patterns of resource partitioning among predators can result from evolutionary divergence among competing species (MacArthur and Levins, 1967; Connell, 1980). Given the widespread effects of anthropogenic activities on food webs, the human-induced rewiring of trophic interactions can reshape interspecific competition patterns and lead to novel forms of resource partitioning (Baum and Worm, 2009).

We combined data on fishing patterns and trophic interactions to assemble a coastal marine food web subject to intensive fishing in the tropical Pacific Ocean. Our goals were to (1) describe the food web structure and the topological roles species and fisheries play; (2) assessing whether fisheries and keystone predators have redundant or complementary interaction patterns; (3) determine how anthropogenic threats vary according to species roles; and (4) assess potential effects of species extinctions and restrictions on fisheries, on food web structure and species roles.

MATERIALS AND METHODS

Species-interaction data

We obtained species-interaction data from stomach contents of species caught by shrimp fisheries in the coast of Colombia [2° 45’N, 78° 10’0W – 3° 50’N, 77° 20’W; see Navia *et al*. (2016) and Figure S3]. We assembled data from 11,203 stomachs of 59 predator species and found 301 prey species (Table S1).

Artisanal and industrial fleets and their catches

We added small-scale fisheries (SSF) and large-scale fisheries (LSF) as additional nodes, and their catches as additional links in the network. Small-scale fisheries encompass various fishing gears, including bottom trawls used by shallow-water shrimp fisheries, hand lines, longlines, gillnets and beach seines. Large-scale fisheries include exclusively deep-water shrimp fisheries (Gallardo *et al*., 2018). Both SSF and LSF primarily target shrimps, and their bycatches encompass many fish and invertebrate species. We used only presence/absence interaction data because information on species abundance, biomass, and catch rates are currently unavailable for the study area.

Network structure

We summarized species-interaction data in an adjacency matrix, **A**, depicting all trophic interactions and fishing targets. The element a_{ij} of **A** is 1 if species *i* and *j* interact and 0 otherwise. We computed the trophic level (TL) for each species using data from the literature and the databases *Fish Base* (Froese and Pauly, 2018) and *Sea Around Us* (www.seaaroundus.org). We categorized trophic levels as TL 1: <2, TL 2: 2.00–2.50, TL 3:

2.51–3.00 (lower trophic levels); TL 4: 3.01–4.00 (intermediate trophic levels) and TL 5: >4.01 (higher trophic levels). We used Gephi 0.9.2 (Bastian *et al*., 2009) and Network Splitter 3D by A. Barão (https://gephi.org/plugins/#/plugin/network-splitter-3d) to draw food webs. We computed connectance as $C = L/S^2$ (Martinez, 1992), where L is the number of observed interactions and S is the number of nodes. We computed modularity metric M (Newman and Girvan, 2004) combined with the simulated annealing optimization algorithm (Guimerà and Amaral, 2005; see the Supplementary material for details).

Species roles

We used two approaches to characterize the role of species and fisheries in the network structure. First, combined the standardized within-module degree (z) and among-module connectivity (c) to define the role of a node I (Guimerà and Amaral, 2005, see the Supporting material for thresholds). Second, we used two centrality metrics (Freeman, 1978) as a proxy for each species influence on the network. Specifically, we used (i) closeness centrality (CC), which describes the shortest paths from a given node to all other nodes to describe the influence of a given node in terms of short indirect pathways to other species in the network; and (ii) betweenness centrality (BC), which depicts how often a node i belongs to the shortest path between nodes j and k (Freeman, 1978) and describes the influence of a node as their participation in the pathways connecting nodes in the network. We used UCINET IV (Borgatti *et al*., 2002) to compute CC and BC.

Threat statuses and species contribution to network structure

To investigate the relationship between a species' threat status and its contribution to network structure, we used threat statuses from the IUCN red list (IUCN, 2020) and the

Colombian national conservation status (Ardila *et al*., 2002; Chasqui *et al*., 2017), when available. The Colombian threat categories are relevant because species may be threatened only at the national level (Table S1). We merged the “vulnerable” and “near-threatened” statuses into a single “higher risk” category. We included species under the status “least concern” in the “lower risk” category as these widespread and abundant taxa are unlikely to die out in the near future (IUCN, 2020).

We performed a principal component analysis (PCA) on the correlation matrix among node degree (D_i), within-module degree (z_i), and among-module connectivity (c_i). Subsequently, we used the resulting first principal component as a proxy for species contributions to network structure, U (Estrada, 2007; Sazima *et al*., 2010; Vidal *et al*., 2014). This approach provides a metric that synthetically describes several aspects of species contributions to network structure (see Costa *et al*., 2007). We investigated the relationship between threat statuses and species contributions to network structure using a two-sample randomization test (Manly, 1997; see the Supplementary material).

Interaction similarity and indirect effects

We computed Jaccard’s similarity index (Jaccard, 1912) to describe pairwise similarities in dietary items between fisheries and all the species within the food web (See Supplementary material). Complementarily, we computed the topological overlap index, TO^3 (Jordán, 2009), to describe the trophic overlap between species based on their indirect pathways (see Supplementary material for details). We computed TO^3 using CoSBiLab Graph (Valentini and Jordán, 2010).

Simulations of species extinctions and fishery regulations

We used simulations to assess the potential impacts of (i) species extinctions and (ii) fishery regulations on food web structure. We removed only one focal node (SSF, LSF or a given species) and its interactions from the food web in each simulation scenario. Following the removal of the focal species and its links, we re-computed modularity (*M*), within-module degree (z_i), and among-module connectivity (c_i). Thus, our extinction scenarios encompassed species belonging to all possible combinations of species roles and trophic levels (Table S2 and S3). Whenever possible, we simulated the extinction of fishing target and non-target species for each trophic level and topological role, one species at a time (Gallardo *et al.*, 2018, Supplementary material). To simulate restrictive regulations on fisheries, we performed additional simulations removing small- and large-scale shrimp fisheries independently. Finally, we simulated a catastrophic extinction event simultaneously involving all 11 species previously removed (independently) belonging to all trophic levels and topological roles (Tables S2 and S3).

RESULTS

Food web structure

The food web without fisheries encompasses 360 species and 985 interactions. When we incorporated small- and large-scale fisheries and their catches, the number of links in the food web increased to 1,090. The food web with fisheries had a higher average number of interactions per node (3.01 vs 2.74) and connectance (0.0083 vs 0.0076) than its counterpart without fisheries. The incorporation of fisheries as nodes led to a slight reduction in modularity, but both networks are significantly modular (*M*=0.51 without fisheries and *M*=0.47 with fisheries $p<0.001$, $n = 500$ randomizations). The food web without fisheries has 7 modules whose sizes range between 25 and 95 taxonomic units, whereas the food web with fisheries has 9 modules ranging from 14 to 68 entities each (Table 1; Figure 1*A* and *D*).

Species roles

Network hubs include a few predator species (less than 2% of the food web) and small-scale fisheries (Figure 1C and F). In the food web without fisheries, network hubs encompass two *Sphyrna* hammerhead sharks, the Smooth-Hound shark *Mustelus lunulatus* and the brown sole *Achirus klunzingeri*. By including small-scale fisheries, the Smooth-Hound shark *Mustelus lunulatus* lost its status as a network hub, whereas the round stingray *Urotrygon rogersi* become one network hub, joining the brown sole and the two hammerheads. Network hubs connect the food web in distinct ways, as indicated by the fact that, in both cases, most network hubs belong to different modules (Figure 1*C* and 1*F*) and by the variation in centrality across network hubs. Small-scale fisheries and two hammerhead sharks show markedly higher betweenness and closeness centralities (Table S1).

Module hubs are highly connected to species within a given module but have few connections with the rest of the network. They represent less than 4% of the species in both types of food webs. The similarity between food webs with and without fisheries extends to the taxonomic composition and trophic levels of module hubs, encompassing species of shrimps, bony fishes, and sharks (Figure 1*C* and *F;* Table S1).

About 10% of the species are connectors that link modules. Connectors include the crab *Callinectes arcuatus*, the shrimp *Solenocera agassizi*, the sharks *Sphyrna tiburo* and *M. henlei*, many pelagic species, and large-scale fisheries (Figure 1; Table S1). Connectors show contrasting dietary preferences that define complementary paths connecting the food web.

Peripheral species with few connections comprise most of the network (85% of the species, Figure 1*B*, 1*E*, Table S1 and Figure S1*A*, *B*).

Several fishery targets change their roles when the network encompasses fisheries. As small-scale fisheries increase among-module connectivity, many peripheral bony fish species of commercial interest become connectors in the network with fisheries (Table S1). In contrast, fisheries also change the roles of many invertebrate species from connectors to peripherals. Accordingly, generalist predators, such as *M. lunulatus*, *S. corona*, change their roles from network to module hubs. Conversely, *S. lewini* and *U. rogersi* change from module hubs to network hubs, likely due to fisheries adding network pathways that do not occur naturally.

Both networks have the most primary producers (TL1) within one single module. Primary and secondary consumers (TL2-TL4) are often module hubs. Top predators and fisheries (TL5) interact with most of the modules as network hubs or connectors (Figure S2*A* and *B*). Mesopredators (TL3 and TL4) are mostly connectors and peripherals (Figure S2*C* and *D*).

Threat statuses and species contribution to the food web structure

The species with higher contributions to network structure (*U*, Table S1) are also those facing the most severe threats (Test Statistic = 3.012; *P* <0.05; Figure 2*B*). For example, the network hub *S. lewini* and the module hub *M. lunulatus*, both nationally threatened in Colombia, with the former also being critically endangered globally, show markedly high contributions to network structure. The same occurs with many module hubs (Figure 1*C*, 2*A*). Conversely, in our study system, many species under low threat levels play peripheral topological roles (Figure 2*A* and *B*).

The similarity in interaction patterns between fisheries and top predators

Small-scale fisheries and large sharks have similar topological roles (Figure 1*C*). However, they show low dietary similarity, suggesting that network hubs are functionally complementary and connect the food web via different direct interactions (Figure 3*A* and *B*). Small-scale fisheries exploit 66 taxa, whereas the hammerhead sharks *S. lewini* and *S. media* prey on 65 and 48 taxa, respectively. Large-scale fisheries (a connector) exploit 39 taxa. These complementary interaction patterns do not imply isolated network hubs. In fact, indirect pathways connect the fisheries and shark in the system, as indicated by the high trophic overlap index (TO^3) among small- and large scale fisheries (SSF=0.31 and LSF=0.24) and the shark *S. lewini* (0.08). In contrast, peripheral species have lower degrees of overlap in their indirect effects (Table S1).

Simulations of species extinctions and fishery regulations

In our simulations, species extinctions did not change modularity. The relative frequencies of topological roles remained similar regardless of the biological and economic roles of the species dying out (Table S2). For example, small-scale fisheries remain a network hub in most scenarios (Table S4). However, the identities of species playing each structural role change following extinctions. For instance, distinct species of *Sphyrna* sharks emerged as network hubs after simulated extinctions (Table S2). The complementary simulation considering the joint extinction of 11 species resulted in only one fish species -- the stingray *U. rogersi* -- and small-scale fisheries remaining as the network hubs (Table S4). Removing shallow-water shrimp fisheries did not change food web modularity and the frequencies of topological roles.

Discussion

Anthropogenic competition as a candidate mechanism underlying resource partitioning

Competition avoidance likely underlies the structure of other marine food webs in which keystone sharks belong to distinct modules (Rezende *et al*., 2009). Empirical evidence supports that fisheries compete with top predators in coastal ecosystems (e.g., Yodzis, 2001; Pichegru *et al*., 2009). We show evidence of resource partitioning between fisheries and hammerhead sharks in a tropical marine food web, reinforcing the notion that competition avoidance influences the organization of this community (Galindo *et al*., 2021).

One may expect that both sharks and fisheries should behave adaptively. Fisheries can behave as adaptive foragers to optimize catch rates (Bertrand *et al.*, 2007). Adaptive fishing strategies include shifts in target species to maximize benefits (Sethi *et al.*, 2010), analogous to the adaptive rewiring of ecological networks (Raimundo *et al*., 2018). However, small-scale fisheries do not rewire their interactions via adaptive target shifts in the study region. These fleets are non-selective and use multiple species, responding to variation in resource availability via changes in fleets size and fishing efforts (Rueda *et al.*, 2012). Hammerhead sharks, therefore, may be forced into suboptimal dietary choices imposed by competition with small-scale fisheries, which act as dominant supergeneralist predator overcoming the other highly connected species.

We acknowledge that inferring interspecific competition from resource use patterns alone can be misleading (Pichegru *et al*., 2009). Alternatively, opportunistic foraging of sharks in distinct habitats could explain the same pattern (Navia *et al*., 2017). On the other hand, fishing has been intensive in the region for decades, and hammerhead sharks are becoming increasingly rare (Navia and Mejía-Falla, 2016). Studies in nearby no-take zones can test our hypothesis that anthropogenic competition shapes resource partitioning. For sites where fishing is banned, we predict hammerhead sharks prey on redundant prey species, including dozens of species monopolized by fisheries outside no-take areas. Testing this hypothesis is relevant because it can advance our understanding of contemporary dynamics of anthropogenic food webs based on general theories that explain how competitive divergence acts as a fundamental mechanism shaping community structure (MacArthur and Levins, 1967; Connell, 1980).

Hyper-hubs and their effects

We propose the concept of "hyper-hub", referring to nodes -- small-scale fisheries and hammerhead sharks – feeding on all topological roles, including other network hubs. Hyper-hubs represent hyperconnected species particularly likely to impose pervasive top-down effects (Navia and Mejía-Falla, 2016). The concept of hyper-hub connects the network approach and the idea that humans act as *hyperkeystone* species whose impacts on other keystones taxa trigger cascading effects that spread rapidly at the ecosystem level (Worm and Paine, 2016).

Hyper-hubs have highly overlapping indirect effects, as described by the trophic overlap index, despite their dissimilar direct interactions. Overlapping indirect interactions arise from high centrality values of a few nodes combined with short average path length within the network. Consequently, the extinction of a *Sphyrna* hyper-hubs will rapidly affect not only its resources but other hyper-hubs and their prey through indirect effects. It remains unclear if such indirect effects will positively or negatively affect species abundances across trophic levels. There is, however, empirical evidence that the demographic decline of *Sphyrna* sharks is likely affecting a wide variety of taxa, including bony fishes, squids, and shrimps (Galindo *et al*., 2021).

By now, our study reinforces the notion that the conservation of *Sphyrna* sharks can promote the long-term persistence of marine biodiversity in the Colombian Pacific (Dulvy *et al*., 2014; Chasqui *et al*., 2017). The higher vulnerability of central species raises concerns regarding the imminent functional disruption of food webs due to anthropogenic extinctions. Non-selective fisheries may be imposing strongly asymmetrical competitive pressures on the progressively rare hammerhead sharks (Puentes *et al*., 2014; Navia and Mejía-Falla, 2016). In this context, our study reinforces a pattern described for some terrestrial ecosystems (Vidal *et al*., 2014) that the positive correlation between species vulnerability to extinction and their contribution to network structure (Figure 2).

Simulations of extinctions and fishery regulations

Our simulations contribute to the assessment of how extinctions and fishery regulations can affect this food web. The simulations show small-scale fisheries remain as a network hub regardless of which species die out. Network structure did not change after removing species belonging to all trophic levels and topological roles, including hyper-hubs. Also, the removal of shallow-water shrimp fisheries did not affect modularity. We should take these results, suggesting a high structural resilience of the food web to extinctions and fishery regulations, cautiously. Our simulations did not incorporate the dynamics of species abundances and interaction rewiring arising from competitive release (Raimundo *et al.*, 2018), which may propagate the impact of extinctions and regulations via cascading effects. In this context, the identity of species acting as network hubs often changes after simulated extinctions.

When we removed top predators showing high topological centrality from the network, species from intermediate trophic levels, such as *M. lunulatus* and *S. tiburo,* emerge as network hubs. Previous studies (Myers *et al*., 2007; Baum and Worm, 2009; Navia *et al*., 2010) support this finding and corroborate the notion that generalist mesopredators can play critical roles in food web dynamics under anthropogenic disturbances (Amariles *et al*., 2017; Galindo *et al*., 2021). Consequently, functional redundancy among generalist mesopredators can buffer the effects of extinctions of top predators (Navia *et al*., 2010). Understanding the mechanisms shaping changes in species' topological roles is critical to predicting how anthropogenic processes affect food webs (D´Alelio *et al*., 2019). Species' traits, such as body size and mobility, often underly modularity (Olmo Gilabert *et al*., 2019). Understanding how such traits mediate species' roles is a problem that deserves further investigation.

Implications for conservation and fishery management strategies

Our results suggest that conservation efforts should extend beyond commercial species, which are primarily peripheral network nodes. Considering the complementarity of direct interactions and the intertwined indirect effects of hyper-hubs, the demographic rescue (*sensu* Carlson *et al*., 2014) of the hammerhead sharks *S. lewini* and *S. media* are likely to rapidly propagate across the food web and reshape patterns of interactions and species abundances. However, the direction and magnitude of such changes remain to be understood.

Beyond describing how hyper-hubs can impose top-down control via direct or indirect effects, our study corroborates the notion that bottom-up processes also influence biodiversity patterns in marine food webs (Lynam *et al*., 2017). Notably, the brown sole *A. klunzingeri*, a network hub, appears among the prey consumed by hyper-hubs, suggesting that this mesopredator may play a key role in community dynamics by connecting top-down and bottom-up effects.

Concluding remarks

The impact of non-selective fishing is reshaping the structure and dynamics of tropical marine food webs. Developing countries urgently need to implement innovative scientific programs that combine network modelling and biomonitoring as a two-way road informing ecosystem-based approaches to conservation that extend beyond commercial and flagship species. Citizen science projects involving artisanal fishers can be particularly useful to implement such an approach. For example, participatory projects can use the predictions of ecological models to design experimental measures to reduce bycatches and promote the demographic rescue of endangered populations of hyper-hub species. Field data arising from citizen science projects could assess the predictions and assumptions of networks model underlying conservation strategies.

Our study contributes to the emerging socio-ecological approach to food web modelling. In temperate regions, socio-ecological studies considering the roles of small-scale fisheries within food webs have shown, for example, that their direct adverse effects on top predators are counterbalanced by indirect positive impacts on the biomass of non-harvested species, albeit leading to a drastic decrease in plankton (Ávila-Thieme *et al*., 2021). Another recent model suggests that the overexploitation of species with higher population biomasses can trigger extinction cascades affecting non-target species and threaten biodiversity, ecosystem functions and fisheries (Glaum *et al*., 2020). Such approaches can disentangle the positive and negative effects of fisheries across trophic levels and on non-target species. A fundamental question that remains open is the extent to which trophic cascades induced by fisheries are common in tropical systems, where top and mesopredator species can show complementary direct interactions but highly overlapping indirect effects.

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Conflict of interest

The authors have no conflict of interest to declare.

Author contribution

VMV, AFN, RSR, PRG, and RLGR conceived and designed the work. VMV compiled datasets from the literature and performed laboratory work, for which AFN provided materials and guidance. VMV, RLGR, and AFN analysed the data. VMV, RLGR, AFN, PRG, and RSR interpreted the results. VMV and RLGR wrote the paper and led the revisions, and AFN, RSR, and PRG contributed to several drafts of the manuscript.

Data availability statement

The data that support the findings of this study are available in the Supplementary Material of this article.

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Tables

Table 1. Structure of a tropical marine food web in the Colombian coast. Network metrics depict two alternative network constructions, one with and another without small and large-scale fisheries and their catches as additional nodes and links. *$P < 0.001$

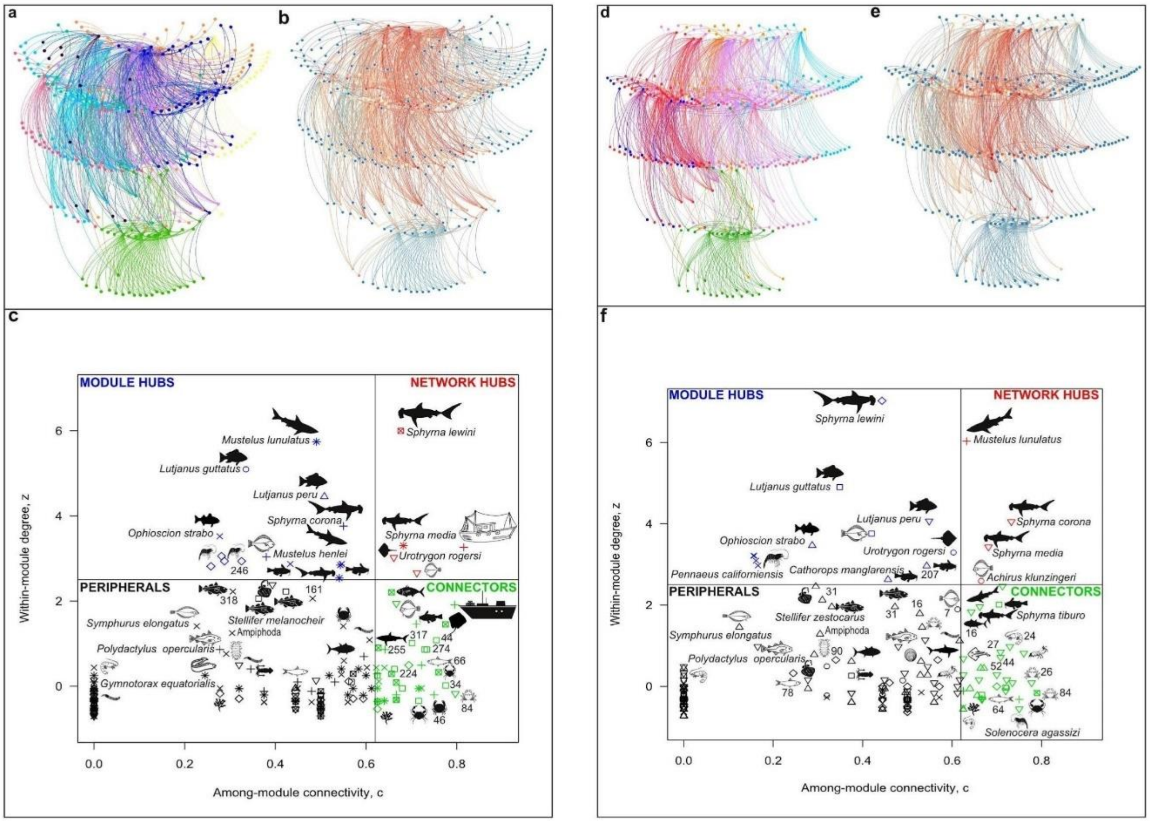
Descriptors	Food web with fisheries	Food web without fisheries
Number of nodes (S)	362	360
Number of links (L)	1090	985
Average links per species (L/S)	3.01	2.74
Connectance	0.0083	0.0076
Number of modules	9	7
Modularity (M)	0.47*	0.51*
% Network hubs	1.38	1.11
% Module hubs	3.87	3.33
% Connectors	11.33	10.28
% Peripherals	83.43	85.28

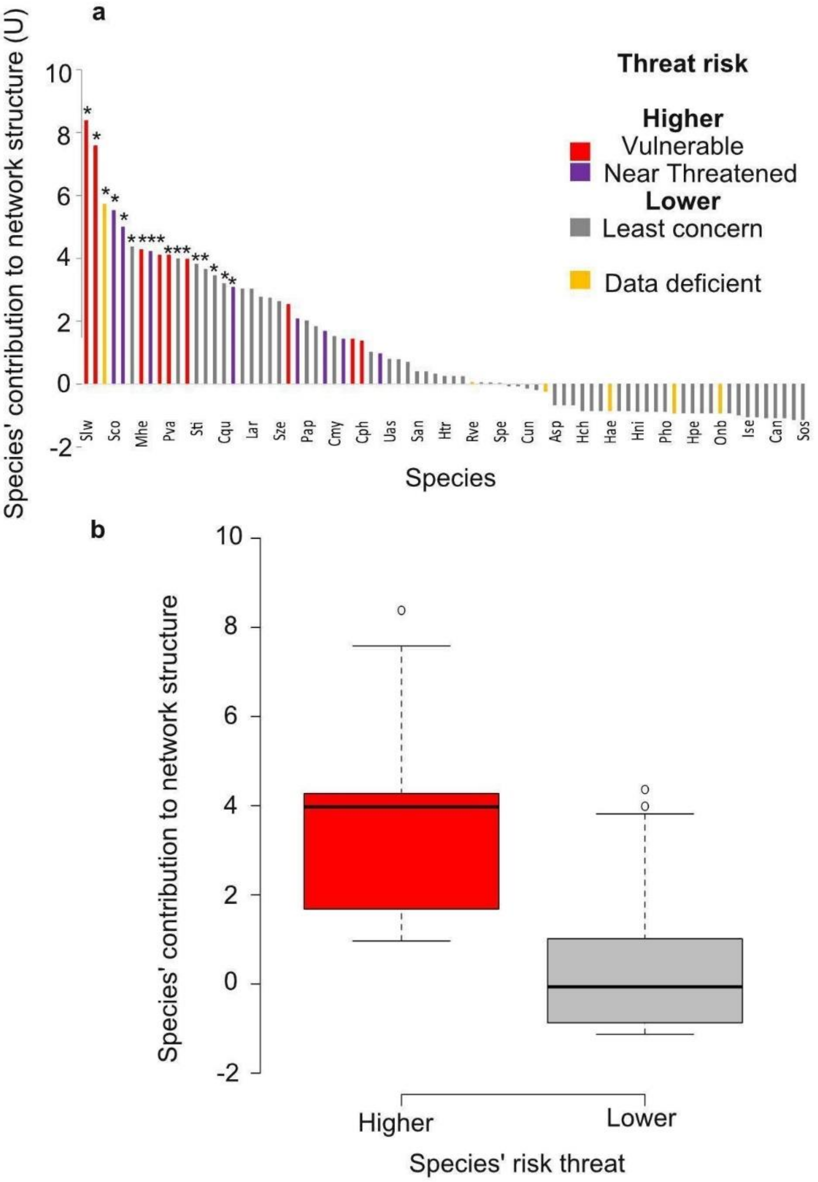
Figure legends

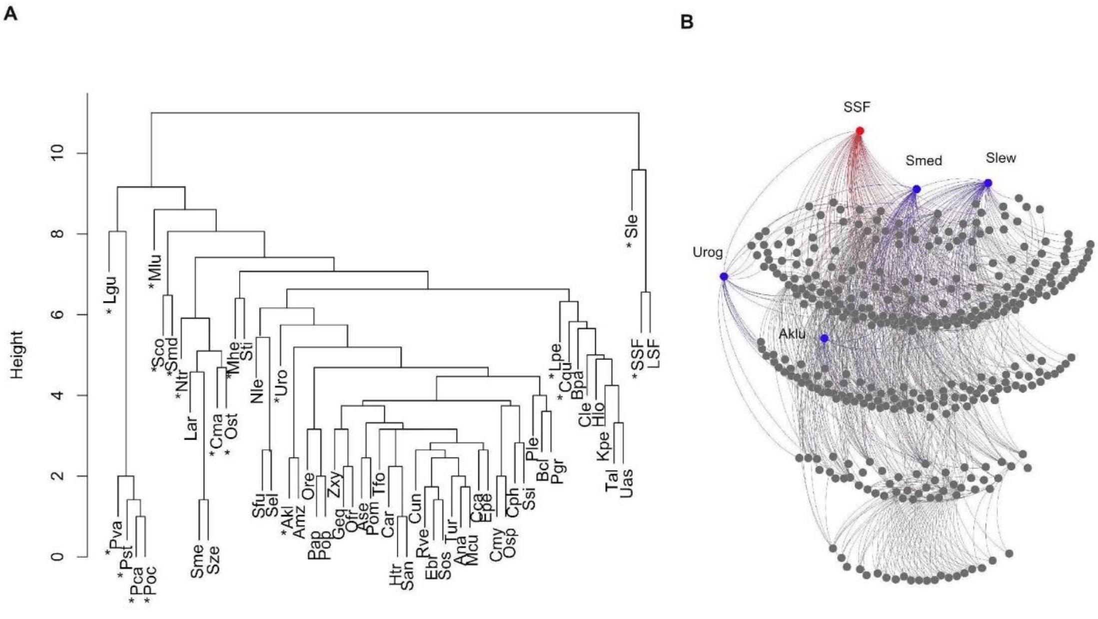
Figure 1. The modular structure of the coastal food web in the tropical Pacific region organized according to species' trophic level and interaction patterns. Food webs with (*A* and *B*) and without (*D*-*E*) fisheries and their catches as additional nodes and links. The colors of the nodes and links correspond to the modules to which each species belongs (*A* and *D*) and their among-module connectivity (*B* and *E*). In the temperature scale used for *B* and *E*, cold and hot colors indicate, respectively, low and high intermodular connectivity. The plots shown in *C* and *F* describe the topological roles of species within the network as defined by the coordinates (c, z) that depict the balance between intermodular connectivity (c) and intramodular connectivity (z). The point for each species is colored according to its topological role, which can be: networks hub (red, high values of both intra- and intermodular connectivity), module hubs (blue, high intramodular connectivity but low intermodular connectivity), connectors (green, low intramodular connectivity but high intermodular connectivity) or peripheral (black, low values of both intra and intermodular connectivity). The symbols in *C* and *F* identify the module to which species belong. The complete list of species names is provided in the Supplementary material, Table S1.

Figure 2. (*A*) Species' contribution to network structure and threat statuses according to IUCN's Red List criteria. (*B*) Species' contribution to network structure (mean ± SE), comparing species sets with contrasting threat statuses (higher vs lower). Asterisks denote network and module hubs.

Figure 3. (*A*) Pairwise dietary similarity between predators as informed by the Jaccard index. Asterisks denote network and module hubs. (*B*) Food web with fisheries, highlighting the interactions of small-scale fisheries (red) and of predator species that also act as network hubs (blue). Grey nodes depict all other topological roles. SSF: small-scale fisheries, Smed: *Sphyrna media*, Slew: *Sphyrna lewini*, Urog: *Urotrygon rogersi*, Aklu: *Achirus klunzingeri*


a
b
c
MODULE HUBS
NETWORK HUBS
PERIPHERALS
CONNECTORS
Mustelus lunulatus
Sphyrna lewini
Lutjanus guttatus
Lutjanus peru
Sphyrna corona
Ophioscion strabo
Sphyrna media
Urotrygon rogersi
Mustelus henlei
246
318
161
Symphurus elongatus
Stellifer melanocheir
Ampiphoda
Polydactylus opercularis
Gymnotorax equatorialis
317
255
44
274
224
66
34
84
46
Within-module degree, z
Among-module connectivity, c
d
e
f
MODULE HUBS
NETWORK HUBS
PERIPHERALS
CONNECTORS
Sphyrna lewini
Mustelus lunulatus
Lutjanus guttatus
Lutjanus peru
Sphyrna corona
Ophioscion strabo
Urotrygon rogersi
Sphyrna media
Pennaeus californiensis
Cathorops manglarensis
207
Achirus klunzingeri
31
16
7
Stellifer zestocarus
Ampiphoda
Sphyrna tiburo
Symphurus elongatus
Polydactylus opercularis
90
78
27
24
52
44
26
64
84
Solenocera agassizi
Within-module degree, z
Among-module connectivity, c


a
Species' contribution to network structure (U)
10
8
6
4
2
0
-2
Threat risk
Higher
🟥 Vulnerable
🟪 Near Threatened
Lower
⬜ Least concern
🟨 Data deficient
Slw
Sco
Mhe
Pva
Sti
Cqu
Lar
Sze
Pap
Cmy
Cph
Uas
San
Htr
Rve
Spe
Cun
Asp
Hch
Hae
Hni
Pho
Hpe
Onb
Ise
Can
Sos
Species
b
Species' contribution to network structure
10
8
6
4
2
0
-2
Higher
Lower
Species' risk threat


A
B
Height
0
2
4
6
8
10
*Pva
*Pst
*Pca
*Poc
*Lgu
*Mlu
*Sco
*Smd
*Ntr
Lar
Sme
Sze
*Cma
*Ost
*Mhe
Sti
Nle
Sfu
Sel
*Uro
*Akl
Amz
Ore
Bap
Pob
Zxy
Geq
Ofr
Ase
Pom
Tfo
Car
Htr
San
Cun
Rve
Ebr
Sos
Tur
Ana
Mcu
Cca
Epe
Cmy
Osp
Cph
Ssi
Ple
Bcl
Pgr
*Lpe
*Cgu
Bpa
Cle
Hlo
Kpe
Tal
Uas
*Sle
*SSF
LSF
SSF
Smed
Slew
Urog
Aklu

Supplemental material

Materials and Methods

Study area. The Colombian Pacific coast has a narrow continental shelf. Extensive mangrove forests (mainly *Rhizophora* spp.) prevail in the southern region (Castellanos-Galindo et al., 2015) and rocky shores in the northern parts of the region, which has few coral reefs (Glynn & Ault, 2000). Fisheries performed along the Central Colombian coast contribute to up to 80% of nationwide catches (Díaz et al., 2011). Although fishing intensity in the region has been decreasing since the 1990s (Lindop et al., 2015), stock assessments estimate that 50% to 67% of target fish species are currently over-exploited (Barreto and Borda, 2008; Barreto et al., 2010; Puentes et al., 2014). Following the decline of fish stocks, industrial fishing decreased accordingly (Baos Estupiñán and Zapata, 2011). The remaining industrial fleets moved into coastal waters to improve their catches (García, 2010). Therefore, more intensive use of coastal waters by industrial fleets adds to existing anthropogenic pressures on marine biodiversity across the central coastline, which has been vital for the Colombian shrimp industry since the 1960s (De la Pava and Mosquera, 2001). Although most fisheries target the shallow-water shrimp species *Penaeus occidentalis* and *Xiphopenaeus riveti*, they also impact many bony fishes, sharks, rays, and invertebrate species via bycatches (Gallardo et al., 2018; Mejía-Falla and Navia, 2011; Navia and Mejía-Falla, 2016).

Food web. We analyzed the stomach contents of fishes from an artisanal bottom trawling fishery named "Changa" (Rueda et al., 2006). We determined the taxonomic identity of dietary items extracted from stomachs to the species level whenever possible. Otherwise, we defined supraspecific taxonomic entities at the genus, family or order levels. Our dataset also includes information on resource use encompassing detritus, phytoplankton, zooplankton, invertebrates, turtles, elasmobranchs, and bony fishes from several published reports between 1990 and 2015 (*Supplementary Appendix* and *References* in Supporting Information). The food web used in this study is more taxonomically resolved than the one previously presented for the Gulf of Tortugas by Navia et al. (2010, 2016). In addition, this study also differs from the latter (Navia et al., 2010; 2016) by considering fisheries and their catches as additional nodes and links in the network.

Network structure. We assessed modularity, *M*, using a module-finding algorithm providing optimal solutions for unipartite graphs (Newman and Girvan, 2004). This algorithm infers the number of modules directly from the interaction structure. The algorithm assigns modules considering those nodes that retain at least 50% of the links within their neighborhoods and computes modularity (*M*) as follows:

$$M = \sum_{s=1}^{N_M} \left[\frac{l_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right] \quad (1),$$

where N_M is the number of modules, L is the number of links in the network, *ls* is the number of links between the nodes of the module, and *ds* is the sum of the degrees of nodes in the module *s*. We used the software MODULAR (Marquitti et al., 2014) to compute *M*. We used the "null model 2" (NM2) proposed by Bascompte et al. (2003) to assess statistical significance. This null model retains the observed heterogeneity of interactions. We then compared the empirical *M*-value to the distribution of the same metric in 500 random networks. In the null model, the interaction probability, P, between the species i and j depends on their degrees (number of interactions):

$$P(i,j) = \frac{1}{2}\left(\frac{k_i}{C} + \frac{k_j}{R}\right) \quad (2),$$

where *k* is the observed number of interactions for the species and R = C, where C is the number of columns and R is the number of rows in the adjacency matrix (Bascompte et al., 2003). Besides assessing modularity, this procedure also provided information on the number and identity of modules as detected by the algorithm.

Species' topological roles. A topological role refers to how interspecific interactions connect a species within and between modules (Guimerà and Amaral, 2005; Olesen, Bascompte, Dupont, and Jordano, 2007). Ecological network studies often use four categories of topological roles: (i) network hubs, which are species with high degrees of intra- and intermodular connectivity and whose removal has widespread structural and dynamical consequences; (ii) module hubs, which show low intermodular connectivity but high intramodular connectivity, i.e., these species have a strong influence on local dynamics but without a global topological impact; (iii) connectors are species showing high intermodular connectivity but low intramodular connectivity, i.e., they provide connections between network compartments; (iv) peripherals are species with low intra- and intermodular connectivity and hence expected to have minimal impacts on community dynamics (Guimerà and Amaral, 2005; Olesen et al., 2007).

The balance between within-module degree (*z*) and among-module connectivity (*c*) define the topological role of each species as a zc-parameter space that can be divided into four regions (Olesen et al., 2007) based on *z* and *c* threshold values (Guimerà and Amaral, 2005). Threshold values are $z = 2.5$, corresponding to a 99% confidence interval, whereas $c = 0.62$ implies that a node has at least 60% of its links within the module (Guimerà and Amaral, 2005). From these thresholds, the following roles are identified: (i) module hubs are species with $z > 2.5$ and $c < 0.62$, i.e., they have high intramodular connectivity but low intermodular connectivity; (ii) connectors are species with $z \leq 2.5$ and $c \geq 0.62$, i.e., they have high intermodular connectivity and low intramodular connectivity; (iii) peripherals are species with $z \leq 2.5$ and $c \leq 0.62$, i.e., they have low intra- and intermodular connectivity, and (iv) network hubs are species with $z > 2.5$ and $c > 0.62$, i.e., they have high intra- and intermodular connectivity and simultaneously act as module hubs and connectors. We used the software Netcarto (Guimerà & Amaral, 2005) to compute *c* and z values for all species.

The standardized within-module degree (*z*, eq. 3*)* refers to the number of links that a species *i* has to other species within its own module (Olesen et al., 2007) and is given by:

$$z = \frac{k_{is} + \underline{k}_s}{SD_{ks}} \quad (3),$$

where k_{is} is the number of links from the species *i* to other species within its own module *s*, whereas $\underline{k}s$ and SD_{ks} are the averages and the standard deviation of within-module links of all species within the module *s*.

Among-module connectivity (*c*, eq.4), also known as the participant coefficient (PC) (Guimerà

& Amaral, 2005), describes the number of interactions of a species *i* with species in other modules (Olesen et al., 2007) and is given by:

$$c = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_t}\right)^2 \quad (4),$$

where k_{it} is the number of links from species *i* to the species in module *t*.

Centrality metrics

The standardized form (CC_i, eq.5) of closeness centrality is given by:

$$CC_i = \frac{N-1}{\sum_{j=1}^{N} \quad d_{ij}} \quad (5),$$

where $i \neq j$, and d_{ij} is the length of the shortest path between nodes *i* and *j*. Closeness is an inverse measure of centrality in that a smaller value of *CC*i indicates a more central node, a node is closer to all other nodes than nodes showing a low value of the metric.

The standardized form for a node *i* (BC_i, eq. 6) is given by:

$$BC_i = \frac{2 * \sum_{j \leq k} \quad g_{jk\frac{i}{g_{jk}}}}{(N-1)(N-2)} \quad (6),$$

where $i \neq j$ and *k*, g_{jk} is the number of equally shortest paths between nodes *j* and *k*, and $g_{jk}(i)$ is the number of shortest paths in which *i* occurs (g_{jk} can be equal to 1). The denominator is twice the number of pairs of nodes without the node *i*. High values of BC_i imply that a node will be more often part of the flows of information within the network compared to nodes with a low value of the metric.

Species extinction risks and contribution to network structure

We performed two-sample randomization tests (Manly, 1997) in which we randomized species' contribution to network structure, *U*, between two categories of threat statuses, higher and lower risk. Subsequently, we calculated the proportion of randomized differences of means equal to or greater than the observed difference of means based on 5,000 randomizations. For the randomization test, we used the EnvStats package available in R (Millard and Kowarik, 2018).

Interaction similarity analysis. To describe pairwise dietary overlaps in the network, we computed the Jaccard similarity index (eq. 7):

$$J_{ij} = \frac{a}{a+b+d} \quad (7),$$

where the interaction similarity between species i and j, J_{ij}. is computed as the number of shared interactions between these species, *a*, divided by the sum of *a*, the number of interactions exclusive to *j* (*b*) and the number of interactions exclusive to *i* (d). The Unweighted Pair Group Method with Arithmetic Mean (UPGMA) defined grouping. We resampled observed similarity values to assess the statistical significance of interaction similarities. In doing so, we performed 100 iterations using the software Bootclus (McKenna, 2003).

Topological overlap index. We followed Jordán (2009) and defined the trophic overlap index, here $T0^3$ (eq. 8) to depict the overlapping indirect effects between nodes *i* and *j*.

$$\sum \mathrm{TO}_{ij}^{n,j} \quad (8).$$

This metric depicts the number of strong interactors (see def below) appearing in both *i*'s and *j*'s effective range, considering a maximal number of steps, *n*, and a threshold, *t*. The effect threshold (*t*) describes the uniqueness of a node's position within the network, i.e., the extent to which it overlaps with its neighbours. Nodes within this range are "strong interactors" receiving effects from node *i* that are greater than *t*. Nodes outside this range are "weak interactors". The sum of TO-values between species *i* and all others ($\sum \mathrm{TO}_{ij}^{n,j}$ summed over all *j* with $i \neq j$) provides the trophic overlap of species *i* (TO_{ij}^{n}). We used a maximum number of steps, $n = 3$, and the threshold $t = 0.15$. The resulting topological overlap ($\mathrm{T0}^3$) between nodes *i* and *j* is the number of strong interactors in the effective range of both nodes (Jordán, 2009).

TABLE S1. Components of the food web in the central-south Colombian Pacific coast. Trophic level (TL). Conservation status (CS) (National or Global; VU: Vulnerable, NT: Near Threat, LC: Least concern, DD: Data deficient, NE: Not evaluated, NA: not applicable). Degree (D). Module (M), Among-module connectivity (*c*). Within-module degree (*z*). Topological roles (TR; P: Peripherals, NH: Network hubs, MH: Module hubs, C: Connectors). Betweenness centrality (BC), Closeness centrality (CC). Topological overlap index (T0^3). The text highlighted in bold show topological roles changing after simulations of extinctions/fishery regulations.

* Species nationally listed

				Without Fisheries					**With Fisheries**							
Node	**Trophic component**	**TL**	**CS**	**D**	**M**	**c**	**z**	**TR**	**D**	**M**	**c**	**z**	**TR**	**BC**	**CC**	**T0^3**
6	*Achirus klunzingeri*	3.2	LC	20	1	0.665	2.59	NH	21	6	0.712	2.66	NH	1902	927	0.02
194	**Mustelus lunulatus*	3.95	VU A4d	58	3	0.633	6.03	**NH**	60	8	0.491	5.74	**MH**	10358	818	0.01
307	**Sphyrna corona*	4.23	NT	44	6	0.732	4.05	**NH**	46	3	0.55	3.76	**MH**	3626	888	0.03
308	*Sphyrna media*	4.13	DD	48	6	0.681	3.43	NH	50	8	0.682	3.30	NH	4964	860	0.02
361	SSF	5							66	3	0.815	3.26	NH	15504	707	0.31
60	*Cathorops manglarensis*	4.3	NE	29	2	0.457	2.63	MH	31	4	0.433	2.87	MH	2333	941	0.02
87	*Cyclopsetta querna*	3.97	LC	20	0	0.42	3.76	MH	22	3	0.38	3.04	MH	1564	953	0.02
245	*Litopenaeus stylirostris*	2.43	VU	36	4	0.157	3.21	MH	38	5	0.281	3.06	MH	2816	891	0
246	**Litopenaeus vannamei*	2.43	VU A4cde	36	4	0.156	3.21	MH	38	5	0.325	2.94	MH	3099	888	0
176	**Lutjanus guttatus*	4.04	NT	30	0	0.349	4.90	MH	31	1	0.335	5.10	MH	7209	953	0.03
177	**Lutjanus peru*	4.02	NT	21	6	0.549	4.06	MH	21	2	0.508	4.45	MH	3209	1032	0
207	*Notarius troschelii*	4.5	LC	36	2	0.543	2.96	MH	37	4	0.546	2.87	MH	2652	934	0.01
222	*Ophioscion strabo*	3.5	LC	31	2	0.287	3.46	MH	32	4	0.277	3.52	MH	2310	944	0
242	*Penaeus californiensis*	2.43	NE	34	4	0.166	2.97	MH	35	5	0.258	2.82	MH	1485	938	0
243	**Penaeus occidentalis*	2.43	VU A4cde	35	4	0.162	3.09	MH	37	5	0.288	2.94	MH	3392	874	0
306	**Sphyrna lewini*	4.24	VU A2a+4d	64	5	0.443	7.02	**MH**	65	7	0.676	6.00	**NH**	9629	819	0.08
353	**Urotrygon rogersi*	3.52	LC	21	1	0.603	3.29	**MH**	22	6	0.661	3.02	**NH**	3178	937	0.01
11	Algae	1	NA	4	4	0.625	-0.51	C	4	5	0.625	-0.53	C	81	1168	0
17	*Anchoa* spp.	3.25	NA	3	0	0.667	-0.20	C	4	3	0.75	-0.20	C	75	976	0
31	*Bagre panamensis*	4	LC	20	0	0.705	2.01	C	22	3	0.711	1.46	C	2023	929	0.01
34	Batrachoididae	3.3	NA	7	6	0.735	0.09	C	7	0	0.776	0.02	C	417	1113	0
44	**Brotula clarkae*	3	NT	12	6	0.708	0.71	C	14	0	0.755	1.08	C	920	933	0

46	Calappidae	3.43	NA	6	1	0.722	-0.03	C	6	4	0.722	-0.05	C	236	1041	0
47	*Callinectes arcuatus*	3.6	NE	9	0	0.79	-0.17	C	9	8	0.716	-0.06	C	762	931	0
49	*Callinectes toxotes*	3.6	NE	3	3	0.667	-0.32	**C**	3	8	0.444	-0.36	**P**	38	1125	0
64	**Cetengraulis mysticetus*	2.47	LC	10	5	0.7	0.00	C	12	3	0.722	0.49	C	601	917	0
52	Crabs	2.6	NA	12	6	0.722	0.16	**C**	12	8	0.583	0.40	**P**	741	954	0
84	Crustaceans	2.7	NA	16	4	0.789	-0.15	C	16	6	0.797	-0.18	C	1717	965	0
151	Hippidae	3.1	NA	3	3	0.667	-0.31	**C**	3	8	0.444	-0.36	**P**	40	1130	0
160	**Katsuwonus pelamis*	4.43	DD	14	6	0.643	1.83	C	16	7	0.656	2.20	C	2179	932	0
165	Leucosiidae	2.6	NA	3	3	0.667	-0.31	**C**	3	8	0.444	-0.36	**P**	20	1125	0
362	LSF	5							39	3	0.796	1.91	C	4765	816	0.24
315	*Michalisquilla parva*	3.5	NE	8	2	0.656	-0.23	**C**	8	8	0.594	-0.21	**P**	341	1002	0
195	**Mustelus henlei*	4.47	VU A4d	34	6	0.713	2.46	**C**	36	8	0.543	2.84	**MH**	3258	930	0.03
230	Palaemonidae	3.14	NA	4	2	0.625	-0.56	**C**	4	0	0.5	-0.54	**P**	45	1091	0
241	Penaeidae	2.43	NA	24	6	0.729	0.98	C	24	0	0.729	0.86	C	1754	852	0
244	*Penaeus* spp.	2.43	NA	10	6	0.7	0.28	**C**	10	8	0.6	0.25	**P**	1146	954	0
122	Phytoplankton	1	NA	6	4	0	-0.03	P	6	5	0.278	-0.18	P	374	1154	0
253	Pleuronectiformes	3.57	NA	4	3	0.75	-0.32	C	4	7	0.625	-0.36	C	52	1016	0
264	Portunidae	2.67	NA	12	6	0.778	0.09	C	12	0	0.625	0.25	C	379	983	0
266	*Portunus* spp.	3.56	NA	10	6	0.66	0.16	C	10	7	0.76	0.33	C	553	968	0
273	*Protrachypene precipua*	2.75	NE	3	6	0.667	-0.32	C	5	3	0.64	-0.35	C	13	959	0
274	*Pseudupeneus grandisquamis*	3.46	LC	12	6	0.708	0.84	C	13	0	0.734	0.86	C	1554	994	0.01
278	**Pseudobatos leucorhynchus*	3.58	VU A4d	12	6	0.625	0.68	C	13	0	0.663	0.40	C	298	944	0
50	Shrimps	2.43	NA	17	2	0.671	0.45	**C**	17	4	0.602	0.44	**P**	1043	881	0
299	*Solenocera agassizii*	2.2	NE	4	6	0.75	-0.56	**C**	5	8	0.56	-0.21	**P**	44	1016	0
301	Solenoceridae	2.51	NA	5	6	0.72	-0.11	**C**	5	8	0.32	-0.06	**P**	69	1049	0
309	*Sphyrna tiburo*	3.95	LC	31	6	0.662	1.96	**C**	32	8	0.541	2.54	**MH**	1798	914	0
313	*Squilla mantoidea*	3	NE	3	6	0.667	-0.32	**C**	3	8	0	-0.21	**P**	21	1096	0

316	*Squilla* sp.	3.5	NA	10	2	0.64	-0.06	C	10	0	0.68	-0.05	C	989	931	0
317	Squillidae	3.5	NA	24	6	0.76	0.81	C	24	0	0.701	1.01	C	2574	824	0
109	Stomatopods	3.5	NA	16	2	0.664	0.45	C	16	4	0.641	0.44	C	937	892	0
345	*Trachypenaeus* spp.	2.72	NA	8	6	0.625	0.28	**C**	9	0	0.568	0.10	**P**	381	977	0
343	Turtles	2.4	NA	3	6	0.667	-0.31	**C**	3	8	0.444	-0.36	**P**	24	1155	0
355	Xanthidae	3.38	NA	4	3	0.625	-0.11	C	4	8	0.625	-0.05	C	113	1125	0
358	*Xiphopenaeus* sp.	2.7	NA	5	0	0.72	-0.03	C	5	8	0.64	-0.35	C	250	1085	0
1	*Abraliopsis* spp.	3.8	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
2	Acanthochiasma	2.21	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
3	Acantholithium	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
4	Acanthometra	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
7	*Achirus mazatlanus*	3.2	NE	14	1	0.612	1.89	**P**	15	6	0.667	1.94	**C**	1021	939	0.01
8	**Aetobatus narinari*	4.17	NT	2	3	0	-0.11	P	2	8	0.5	-0.42	P	5	1289	0
9	Albuneidae	3.1	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
10	Alpheidae	3	NA	3	2	0.444	-0.56	P	3	0	0.444	-0.54	P	12	1253	0
12	*Alpheus* sp.	2.4	NA	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
13	*Aluterus* sp.	2.81	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
14	*Ambidexter panamensis*	3	NE	1	1	0	-0.56	P	1	6	0	-0.58	P	0	1297	0
15	Amphipoda	3.18	NA	16	2	0.305	1.28	P	16	4	0.305	1.25	P	673	1050	0
18	*Anchovia macrolepidota*	2.7	LC	1	0	0	-0.32	P	3	3	0	-0.12	P	1	1014	0
16	*Anchoa spinifer*	4.1	LC	1	0	0	-0.32	P	3	3	0	-0.12	P	1	1014	0
19	*Anchoa starksi*	3.3	NE	1	5	0	-0.49	P	1	3	0	-0.32	P	0	1306	0
20	Anguilliformes	3.89	NA	5	2	0.56	-0.39	P	5	4	0.56	-0.38	P	73	1049	0
21	*Anisotremus* sp.	3.6	NA	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
22	Anomura	2.5	NA	11	2	0.529	0.28	P	11	4	0.545	0.27	P	576	951	0

23	*Aratus pisonii*	3.1	NE	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
24	*Arenaeus mexicanus*	4	NE	4	6	0	0.00	P	4	8	0	-0.06	P	52	1186	0
25	Ariidae	3.48	NA	2	5	0	-0.33	P	2	7	0.5	-0.42	P	0	1150	0
26	*Ariopsis seemanni*	3.78	LC	7	2	0.449	-0.06	P	7	4	0.449	-0.05	P	435	1143	0
27	Ascidians	3	NA	1	1	0	-0.56	P	1	6	0	-0.58	P	0	1287	0
28	Astrolithidae	2.21	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
29	Aulopiformes	4	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1288	0
30	Axiidae	3.43	NA	3	2	0	-0.39	P	3	0	0	-0.38	P	3	1254	0
32	Balistidae	3.25	NA	2	6	0	-0.03	P	2	2	0	-0.05	P	36	1247	0
33	*Bathygobius* sp.	3.7	NA	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
35	Batoidea	3.88	NA	3	6	0.444	-0.33	P	3	7	0.444	-0.36	P	23	1051	0
36	Beloniformes	4.38	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
37	*Benthesicymus tanneri*	3.24	NE	1	1	0	-0.56	P	1	6	0	-0.58	P	0	1297	0
38	Biddulphia	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
39	Bivalves	2	NA	14	2	0.531	0.61	**P**	14	4	0.622	0.44	**C**	515	969	0
40	*Bollmannia chlamydes*	3.5	LC	1	0	0	-0.32	P	1	3	0	-0.57	P	0	1313	0
41	Bothidae	3.77	NA	2	6	0	-0.33	P	2	3	0	-0.36	P	0	1259	0
42	Brachyura	2.6	NA	22	2	0.533	1.45	P	22	4	0.55	1.41	P	1807	866	0
43	*Bregmaceros bathymaster*	3.5	LC	1	6	0	-0.41	P	1	2	0	-0.42	P	0	1392	0
45	Buccinidae	3.06	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
123	Calappidae	3.6	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1343	0
48	*Callinectes* spp.	3.63	NA	4	6	0.5	-0.11	P	4	8	0	-0.06	P	26	1097	0
51	*Cancer johngarthi*	2.7	NE	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1294	0
53	Capitellidae	2.65	NA	2	1	0	-0.21	P	2	6	0	-0.22	P	0	1285	0

54	Carangidae	4.05	NA	2	6	0	-0.33	P	2	3	0	-0.36	P	0	1259	0
55	**Caranx caninus*	4.1	LC	7	5	0.571	0.00	**P**	8	7	0.656	0.29	**C**	497	956	0
56	*Caranx* sp.	4.12	NA	1	0	0	-0.32	P	1	3	0	-0.57	P	0	1289	0
57	*Carcharhinus leucas*	4.31	NT	13	5	0.568	0.65	**P**	13	7	0.627	0.90	**C**	740	928	0.05
59	Carditidae	2.1	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
58	Caridea	3.43	NA	4	2	0.375	-0.39	P	4	4	0.375	-0.38	P	57	1184	0
86	Cavoliniidae	2.1	NA	1	6	0	-0.41	P	1	2	0	-0.42	P	0	1392	0
62	*Centropomus unionensis*	3.9	LC	4	2	0.375	-0.39	P	4	4	0.375	-0.38	P	18	1167	0
61	Cephalopods	3.84	NA	11	6	0.545	0.49	P	11	8	0.545	0.40	P	666	933	0
63	Ceratium	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
65	Chaenopsidae	3.53	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1343	0
66	Chaetoceros	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
67	Chaetognats	2.21	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
68	*Chloroscombrus orqueta*	2.54	LC	1	5	0	-0.49	P	3	3	0.444	-0.35	P	10	975	0
69	*Chloroscombrus* sp.	2.5	NA	1	6	0	-0.41	P	1	7	0	-0.42	P	0	1292	0
70	*Chromis* spp.	3.77	NA	1	6	0	-0.32	P	1	3	0	-0.51	P	0	1248	0
71	Cyanobacterias	1	NA	1	4	0	-0.63	P	1	5	0	-0.65	P	0	1251	0
72	Cirratulidae	2.65	NA	3	1	0.444	-0.56	P	3	6	0.444	-0.54	P	25	1285	0
73	Cirripedians	2.7	NA	1	6	0	-0.49	P	1	7	0	-0.42	P	0	1292	0
74	*Citharichthys gilberti*	3.46	LC	1	0	0	-0.32	P	3	3	0	-0.12	P	1	1014	0
75	Cladocerans	2.7	NA	2	2	0	-0.56	P	2	4	0	-0.54	P	0	1327	0
76	*Cloridopsis dubia*	3.5	NE	2	3	0.5	-0.31	P	2	8	0.5	-0.51	P	12	1143	0
77	Clupeidae	3.2	NA	4	6	0	0.00	P	4	3	0	-0.06	P	13	1136	0
78	Clupeiformes	3.24	NA	7	5	0.245	0.32	P	7	7	0.571	0.29	P	126	1053	0
79	Cnidarians	3.46	NA	3	1	0.444	-0.21	P	3	6	0.444	-	P	14	1166	0

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80	Congridae	3.92	NA	2	5	0	-0.33	P	2	7	0.5	-0.32	P	25	1164	0
81	Copepods	2.7	NA	11	2	0.496	-0.15	P	11	5	0.562	0.11	P	430	1043	0
82	Corallanidae	2.7	NA	4	2	0	-0.23	P	4	0	0	-0.21	P	11	1227	0
83	Coscinodiscus	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
85	Cumacea	2.7	NA	5	2	0	-0.06	P	5	4	0	-0.05	P	24	1238	0
341	Collodaria	2.21	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
89	Cynoglossidae	3.28	NA	4	6	0.375	-0.17	P	5	3	0.32	-0.06	P	81	979	0
92	*Cynoscion analis*	4.06	LC	1	0	0	-0.32	P	1	3	0	-0.57	P	0	1289	0
90	**Cynoscion phoxocephalus*	3.8	VU A1bd	10	5	0.34	0.65	P	11	3	0.595	0.70	P	686	946	0
91	*Cynoscion* sp.	4.21	NA	2	0	0.5	-0.32	P	2	8	0.5	-0.57	P	6	1256	0
199	Decapoda	3.14	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1503	0
338	Decapodiformes	3.9	NA	4	6	0.375	-0.17	P	4	8	0.375	-0.21	P	34	1041	0
93	Dendrobranchiata	3.24	NA	3	3	0.444	-0.11	P	3	8	0.444	-0.36	P	66	1116	0
94	Detritus	1	NA	7	4	0.571	-0.27	P	7	5	0.571	-0.30	P	173	1145	0
95	*Diapterus* sp.	3.38	NA	1	0	0	-0.20	P	2	1	0.5	-0.20	P	0	1037	0
96	Diatoms	1	NA	3	5	0.444	-0.51	P	3	5	0.444	-0.12	P	7	1186	0
97	Dinoflagellates	1	NA	2	5	0.5	-0.63	P	2	5	0	-0.12	P	0	1265	0
98	Diogenidae	4	NA	3	2	0	-0.39	P	3	4	0	-0.38	P	11	1243	0
99	*Diplectrum*	3.99	NA	1	6	0	-0.41	P	1	2	0	-0.42	P	0	1392	0
100	Ditylum	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
101	Dorippidae	2.6	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
167	*Doryteuthis (Amerigo) gahi*	4.2	NE	1	0	0	-0.32	P	1	3	0	-0.57	P	0	1313	0
102	*Dosidicus gigas*	4.14	DD	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0

103	Drilonereis	2.65	NA	1	2	0	-0.73	P	1	6	0	-0.70	P	0	1319	0
108	Echinoderms	2.3	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
105	*Echiophis brunneus*	4	LC	4	5	0	0.00	P	4	7	0.5	-0.12	P	42	1124	0
106	*Emerita* sp.	3.1	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1304	0
107	Engraulidae	3.2	NA	7	6	0.449	0.16	P	7	3	0.449	0.10	P	89	993	0
110	*Ethusa ciliatifrons*	2.6	NE	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
111	*Eucinostomus* spp.	3.03	NA	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
112	*Eugerres brevimanus*	3.4	LC	6	5	0.5	0.00	**P**	6	7	0.667	0.09	**C**	450	1055	0
104	*Eugerres lineatus*	3.4	NE	1	6	0	-0.41	P	1	7	0	-0.42	P	0	1292	0
113	*Eunice* sp.	2.65	NA	1	2	0	-0.73	P	1	6	0	-0.70	P	0	1319	0
114	Eunicidae	2.65	NA	3	1	0.444	-0.56	P	3	6	0.444	-0.54	P	23	1238	0
115	Euphausiacea	2.2	NA	5	2	0	-0.06	P	5	4	0	-0.05	P	15	1226	0
116	*Euphylax robustus*	2.67	NE	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
117	*Euphylax* sp.	4	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
118	*Eurypanopeus transversus*	2.6	NE	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
119	Exocoetidae	3.57	NA	1	6	0	-0.41	P	1	2	0	-0.42	P	0	1392	0
164	Flatfishes	3.57	NA	1	6	0	-0.41	P	1	2	0	-0.42	P	0	1392	0
121	*Fistularia* sp.	4.5	NA	1	6	0	-0.41	P	1	7	0	-0.42	P	0	1292	0
124	Galatheidae	3.1	NA	3	6	0.444	-0.03	P	3	2	0.444	-0.05	P	41	1210	0
125	Gammaridea	3	NA	3	2	0	-0.39	P	3	4	0	-0.38	P	8	1246	0
126	Gastropoda	3.06	NA	11	2	0.545	0.28	**P**	11	4	0.628	0.11	**C**	455	1075	0
127	Gigartaconidae	2	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
128	Glycera	2.65	NA	1	2	0	-0.73	P	1	6	0	-0.70	P	0	1319	0
129	Glyceridae	2.65	NA	5	1	0.32	0.49	P	5	6	0.32	0.50	P	115	1175	0
130	Gobiidae	3.11	NA	1	6	0	-0.31	P	1	8	0	-	P	0	1290	0

												0.51				
131	*Gonatus onyx*	3.9	LC	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
132	Goneplacidae	2.6	NA	1	6	0	-0.49	P	1	8	0	-0.51	P	0	1516	0
133	Goniada	2.65	NA	1	2	0	-0.73	P	1	6	0	-0.70	P	0	1319	0
134	Goniadidae	2.65	NA	1	2	0	-0.73	P	1	6	0	-0.70	P	0	1319	0
135	*Goniadides* sp.	2.65	NA	1	2	0	-0.73	P	1	6	0	-0.70	P	0	1319	0
136	*Goniopsis pulchra*	2.6	NE	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
137	Gonodactylidae	3.5	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1294	0
138	Gonostomatidae	3.1	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
139	Grapsidae	2.6	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1316	0
140	*Grapsus grapsus*	2.6	NE	2	0	0.5	-0.20	P	2	1	0.5	-0.20	P	62	1232	0
141	*Guyanacaris caespitosa*	3.43	NE	1	6	0	-0.31	P	1	8	0	-0.51	P	0	1290	0
142	*Gymnothorax equatorialis*	4	LC	7	6	0	0.49	P	7	8	0.245	0.25	P	410	1156	0
147	*Haemulopsis nitidus*	3.4	LC	1	0	0	-0.32	P	2	3	0	-0.35	P	0	1042	0
148	*Halichoeres aestuaricola*	3.5	DD	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
143	*Halichoeres chierchiae*	3.5	LC	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
144	*Halichoeres dispilus*	3.9	LC	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
145	*Halichoeres notospilus*	3.5	LC	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
146	*Harengula thrissina*	3.1	LC	4	2	0.375	-0.39	P	5	4	0.56	-0.38	P	29	1008	0
149	*Hepatus kossmanni*	2.6	NE	2	3	0.5	-0.31	P	2	8	0.5	-0.51	P	12	1143	0
150	*Hepatus* sp.	2.6	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
152	*Histioteuthis* cf. *heteropsis*	4.16	NE	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
5	Holacanthida	2.21	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
153	*Hyaloteuthis pelagica*	3.8	LC	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0

154	**Hypanus longus*	3.9	VU A4d	15	6	0.48	0.98	**P**	17	7	0.775	1.45	**C**	1524	932	0
155	*Ichthyapus selachops*	3.8	LC	1	6	0	-0.49	P	1	8	0	-0.51	P	0	1220	0
156	Ichthyoplankton	2.21	NA	3	1	0.444	-0.21	P	3	6	0.444	-0.22	P	11	1276	0
158	Inachoididae	2.6	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
159	Isopoda	3.18	NA	12	2	0.292	0.78	P	12	4	0.292	0.76	P	432	1078	0
161	*Larimus argenteus*	3.1	LC	24	2	0.528	1.79	P	26	4	0.482	2.06	P	1485	955	0.01
162	*Larimus* spp.	3.5	NA	1	5	0	-0.49	P	2	7	0.5	-0.32	P	9	982	0
163	*Leachia danae*	3.9	LC	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
166	*Lile stolifera*	3.49	LC	1	5	0	-0.49	P	3	3	0.444	-0.35	P	1	1030	0
169	Loliginidae	3.9	NA	9	6	0.494	0.32	P	9	3	0.346	0.40	P	217	952	0
168	*Loligo* sp.	3.99	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1343	0
170	*Lolliguncula argus*	3.4	NE	2	6	0.5	-0.32	P	2	8	0	-0.36	P	5	1209	0
171	*Lolliguncula diomedae*	3.25	NE	2	5	0.5	-0.32	P	2	7	0.5	-0.32	P	11	1103	0
172	*Lolliguncula panamensis*	3.9	NE	4	0	0.375	0.26	P	5	3	0.48	-0.12	P	47	1018	0
173	Luciferidae	2.93	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1304	0
174	Lumbrineridae	2.65	NA	1	2	0	-0.73	P	1	6	0	-0.70	P	0	1319	0
175	**Lutjanus argentiventris*	4.07	LC	1	0	0	-0.32	P	2	3	0	-0.35	P	0	1042	0
178	*Lysiosquilla panamica*	3.5	NE	1	6	0	-0.32	P	1	3	0	-0.51	P	0	1248	0
179	*Lysiosquilla* sp.	3.5	NA	2	2	0	-0.56	P	2	0	0	-0.54	P	0	1288	0
180	Lysiosquillidae	3.5	NA	5	2	0.56	-0.39	P	5	4	0.48	-0.38	P	49	1110	0
181	*Macrobrachium americanum*	3.14	LC	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
182	Macroalgae	1	NA	1	4	0	-0.63	P	1	5	0	-0.65	P	0	1248	0
183	*Macrodon mordax*	4.2	DD	1	0	0	-0.32	P	2	3	0	-0.35	P	0	1042	0
184	Majidae	2.6	NA	2	3	0	-0.11	P	2	8	0	-0.36	P	12	1149	0
185	*Meiosquilla dawsoni*	3.5	NE	3	2	0	-0.39	P	3	0	0	-	P	4	1242	0

												0.38				
186	Melosira	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
187	*Metapenaeopsis beebei*	2.43	NE	1	6	0	-0.41	P	1	2	0	-0.42	P	0	1392	0
188	Mollusca	3.44	NA	5	4	0.32	-0.27	P	5	5	0.32	-0.30	P	33	1111	0
189	*Mugil curema*	2.01	LC	1	4	0	-0.63	P	1	5	0	-0.65	P	0	1514	0
190	Mugilidae	2.53	NA	2	6	0	-0.33	P	2	3	0	-0.36	P	0	1259	0
191	Munida	3.1	NA	2	3	0	-0.11	P	2	8	0	-0.36	P	12	1149	0
192	*Munida obesa*	3.1	NE	1	6	0	-0.31	P	1	8	0	-0.51	P	0	1290	0
193	*Muraena* sp.	3.65	NA	1	0	0	-0.32	P	1	3	0	-0.57	P	0	1289	0
196	*Myrophis vafer*	4.2	LC	1	6	0	-0.49	P	1	8	0	-0.51	P	0	1220	0
197	Mysida	3	NA	8	2	0	0.45	P	8	4	0	0.44	P	65	1180	0
198	**Narcine leoparda*	3.2	NT	24	2	0.295	2.46	P	26	6	0.393	2.38	P	3571	959	0.02
200	Navicula	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
201	Nemertea	2.5	NA	2	1	0	-0.21	P	2	6	0	-0.22	P	0	1285	0
202	*Neodoclea boneti*	3.43	NE	1	6	0	-0.32	P	1	3	0	-0.51	P	0	1248	0
203	*Neogonodactylus stanschi*	3.5	NE	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1315	0
204	Nephtyidae	2.65	NA	2	1	0	-0.21	P	2	6	0	-0.22	P	0	1285	0
205	Nereididae	2.65	NA	7	1	0.49	0.14	P	7	6	0.49	0.14	P	124	1161	0
206	Nereis	2.65	NA	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
208	Nucula	2.23	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1415	0
209	*Ocypode* spp.	2.6	NA	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
210	Oenonidae	2.65	NA	1	2	0	-0.73	P	1	6	0	-0.70	P	0	1319	0
211	Ogyrididae	3.43	NA	5	2	0	-0.06	P	5	0	0	-0.05	P	40	1206	0
212	*Ogyrides alphaerostris*	3.43	NE	1	1	0	-0.56	P	1	6	0	-0.58	P	0	1297	0
215	Oligochaeta	2.5	NA	6	4	0.444	-0.27	P	6	5	0.444	-	P	89	1138	0

												0.30				
214	*Oligoplites refulgens*	4.05	LC	6	6	0	0.32	P	8	3	0.531	0.10	P	138	998	0
213	*Oligoplites* sp.	4.05	NA	2	5	0	-0.33	P	2	3	0	-0.12	P	1	1297	0
216	Olividae	2	NA	2	6	0	-0.33	P	2	7	0.5	-0.42	P	3	1216	0
217	*Ommastrephes bartramii*	4.09	LC	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
218	Onuphidae	2.65	NA	3	1	0	0.14	P	3	6	0	0.14	P	21	1223	0
219	*Onychoteuthis banksii*	3.79	DD	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
220	Ophichthidae	3.64	NA	3	6	0.444	-0.03	P	3	2	0.444	-0.05	P	42	1222	0
221	*Ophichthus frontalis*	3.64	LC	5	6	0	0.16	P	5	8	0.32	-0.06	P	24	1162	0
223	*Opisthonema libertate*	2.89	LC	1	0	0	-0.32	P	1	3	0	-0.57	P	0	1289	0
224	*Opisthonema* spp.	2.89	NA	10	5	0.46	0.09	**P**	11	5	0.694	0.49	**C**	503	1005	0
225	*Opisthopterus* sp.	3.16	NA	2	0	0.5	-0.20	**P**	3	3	0.667	-0.20	**C**	15	1012	0
226	Ostracoda	2.7	NA	5	4	0	-0.15	P	5	5	0.32	-0.30	P	14	1156	0
227	*Pachygrapsus transversus*	2.6	NE	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
229	*Palaemon* sp.	2.65	NA	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
228	Palicidae	3.43	NA	1	6	0	-0.41	P	1	0	0	-0.42	P	0	1293	0
232	Pandalidae	2.7	NA	2	2	0.5	-0.31	P	2	8	0.5	-0.70	P	4	1263	0
233	*Panopeus purpureus*	2.6	NE	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
234	*Paradasygyius depressus*	2.6	NE	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
236	Paralichthyidae	4.06	NA	2	2	0.5	-0.32	P	2	3	0.5	-0.70	P	5	1219	0
235	*Paralonchurus petersii*	3.3	LC	2	5	0	-0.33	**P**	3	7	0.667	-0.32	**C**	20	956	0
237	*Parasquilla similis*	3.5	NE	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
238	*Parthenope* sp.	2.6	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
239	Pasiphaeidae	2.43	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1301	0
240	Pectinariidae	3	NA	2	2	0	-0.56	P	2	4	0	-	P	0	1327	0

												0.54				
120	*Penaeus brevirostris*	2.7	NE	2	5	0	-0.33	**P**	3	7	0.667	-0.32	**C**	10	1013	0
247	Perciformes	3.53	NA	3	6	0.444	-0.33	P	3	8	0	-0.21	P	22	1178	0
248	Peridinium	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
157	*Persephona subovata*	2.6	NE	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
249	*Petrolisthes zacae*	3.1	NE	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
250	Phyllodocidae	2.65	NA	1	1	0	-0.56	P	1	6	0	-0.58	P	0	1297	0
251	Phyllostauros	2.6	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
252	Pinnotheridae	2.6	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1294	0
349	Plagiacantha	2.21	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
231	Pleocyemata	3.14	NA	5	2	0	-0.06	P	5	4	0	-0.05	P	15	1226	0
254	Polychaeta	2.65	NA	21	2	0.617	1.12	P	21	4	0.608	1.09	P	1932	897	0
255	*Polydactylus approximans*	3.59	LC	17	6	0.54	1.14	**P**	18	3	0.642	0.86	**C**	1886	912	0.01
256	*Polydactylus opercularis*	3.3	NE	11	6	0.165	0.98	P	12	3	0.278	0.86	P	495	985	0.01
257	Polynemidae	3.62	NA	1	6	0	-0.31	P	1	8	0	-0.51	P	0	1290	0
258	Polyplacophora	2.1	NA	2	2	0	-0.56	P	2	4	0	-0.54	P	4	1275	0
259	Polystira	2.28	NA	1	6	0	-0.49	P	1	7	0	-0.42	P	0	1292	0
260	*Pomadasys panamensis*	3.79	LC	6	2	0.278	-0.06	P	6	4	0.278	-0.05	P	43	1053	0
261	Porcellanidae	3.1	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1343	0
262	*Porichthys margaritatus*	3.3	LC	1	6	0	-0.31	P	2	0	0.5	-0.57	P	0	1021	0
263	*Porichthys* spp.	3.8	NA	2	6	0.5	-0.32	P	2	8	0	-0.36	P	2	1177	0
265	*Portunus asper*	3.56	NE	5	6	0.56	0.09	P	5	8	0	0.10	P	50	1071	0
267	*Portunus xantusii*	4	NE	1	6	0	-0.41	P	1	2	0	-0.42	P	0	1392	0
268	*Prionotus horrens*	3.6	LC	1	0	0	-0.32	P	2	3	0	-0.35	P	0	1042	0
269	Pristigasteridae	3.5	NA	2	5	0	-0.33	P	2	7	0.5	-0.32	P	4	1156	0

270	*Processa peruviana*	2.2	NE	1	1	0	-0.56	P	1	6	0	-0.58	P	0	1297	0
271	*Processa* sp.	2.2	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1301	0
272	Processidae	2.2	NA	2	6	0.5	-0.56	P	2	0	0.5	-0.58	P	6	1252	0
275	Pseudosquillidae	3.5	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
276	Pteropoda	2.28	NA	2	5	0.5	-0.63	P	2	5	0.5	-0.32	P	6	1242	0
277	Pycnogonidae	3	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1329	0
279	*Raja velezi*	3.6	DD	2	6	0	-0.11	P	2	0	0.5	-0.20	P	3	1247	0
88	Ranellidae	2.1	NA	1	6	0	-0.49	P	1	7	0	-0.42	P	0	1292	0
281	Raninidae	2.6	NA	2	3	0.5	-0.41	P	2	2	0.5	-0.42	P	52	1148	0
280	*Raninoides benedicti*	2.6	NE	3	6	0.444	-0.11	P	3	8	0	-0.21	P	21	1130	0
282	Rhizosolenia	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
283	*Rimapenaeus byrdi*	2.51	NE	2	6	0.5	-0.32	P	3	3	0.444	-0.36	P	3	994	0
284	*Rimapenaeus faoe*	2.51	NE	1	6	0	-0.32	P	1	3	0	-0.51	P	0	1248	0
285	*Rimapenaeus fuscina*	2.51	NE	3	6	0.444	-0.33	**P**	4	3	0.625	-0.36	**C**	33	945	0
286	*Rimapenaeus pacificus*	2.51	NE	2	6	0.5	-0.32	P	2	8	0	-0.36	P	2	1177	0
287	*Rimapenaeus* spp.	2.51	NA	3	6	0.444	-0.33	P	4	8	0.375	-0.21	P	8	981	0
289	Sciaenidae	3.76	NA	7	6	0.612	0.00	P	7	8	0.612	-0.06	P	109	1002	0
290	**Scomberomorus sierra*	4.2	NT	6	5	0.444	0.00	**P**	8	3	0.625	0.29	**C**	256	965	0
291	Scombridae	4.26	NA	2	5	0.5	-0.49	P	2	7	0.5	-0.32	P	17	1147	0
292	Scorpaeniformes	3.78	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
293	Scyphozoa	2.1	NA	2	6	0.5	-0.41	P	2	2	0.5	-0.42	P	27	1188	0
294	**Selene peruviana*	4	LC	2	0	0.5	-0.32	P	4	3	0.375	-0.12	P	35	966	0
296	*Sesarma rhizophorae*	2.6	NE	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
295	*Sergia inoa*	2.93	NE	1	1	0	-0.56	P	1	6	0	-0.58	P	0	1297	0

328	*Sicyonia disdorsalis*	3.24	NE	1	1	0	-0.56	P	1	6	0	-0.58	P	0	1297	0
297	*Sicyonia picta*	2.2	NE	1	6	0	-0.41	P	1	2	0	-0.42	P	0	1392	0
329	*Sicyonia* sp.	3.24	NA	3	5	0.444	-0.33	**P**	3	7	0.667	-0.32	**C**	19	1081	0
330	Sicyoniidae	3.24	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1315	0
298	Sipuncula	2.9	NA	7	2	0.449	-0.06	P	7	4	0.449	-0.05	P	235	1014	0
288	*Skeletonema*	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
300	*Solenocera* sp.	2.2	NA	2	2	0.5	-0.49	P	2	0	0.5	-0.70	P	3	1182	0
302	Sphaerozoum	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
303	*Sphoeroides annulatus*	3.1	LC	3	2	0.444	-0.56	**P**	5	3	0.64	-0.35	**C**	31	1009	0
304	*Sphyraena* sp.	4.4	NA	1	6	0	-0.41	P	1	7	0	-0.42	P	0	1292	0
305	Sphyraenidae	4.4	NA	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
310	Spionidae	2.65	NA	4	2	0.375	-0.39	P	4	4	0.375	-0.38	P	23	1290	0
311	*Squilla aculeata*	3	NE	1	6	0	-0.49	P	1	8	0	-0.51	P	0	1274	0
312	*Squilla biformis*	3	NE	2	3	0.5	-0.32	P	3	3	0.444	-0.36	P	13	1021	0
314	*Squilla panamensis*	3.5	NE	9	6	0.617	0.16	P	9	8	0.519	0.25	P	555	1047	0
318	*Stellifer fuerthii*	3.3	NE	22	2	0.31	2.12	P	23	4	0.306	2.22	P	1641	969	0.01
319	*Stellifer melanocheir*	3.3	LC	24	2	0.472	1.96	P	26	0	0.423	2.22	P	1364	930	0.01
320	*Stellifer oscitans*	3.4	LC	1	4	0	-0.63	P	1	6	0	-0.65	P	0	1325	0
321	*Stellifer* sp.	3.4	NA	3	0	0	0.26	P	4	3	0.375	-0.12	P	24	994	0
322	*Stellifer zestocarus*	3.5	LC	21	2	0.331	1.96	P	23	0	0.363	2.06	P	938	958	0
323	*Stenocionops ovatus*	2.6	NE	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
324	*Stenorhynchus debilis*	2.6	NE	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
325	Sternaspidae	2.65	NA	1	6	0	-0.56	P	1	0	0	-0.58	P	0	1354	0
326	*Sthenoteuthis oualaniensis*	4.09	LC	1	5	0	-0.49	P	1	7	0	-0.32	P	0	1179	0
327	*Strongylura* sp.	4.38	NA	1	6	0	-0.41	P	1	7	0	-	P	0	1292	0

												0.42				
331	*Symphurus elongatus*	3.4	NE	15	2	0.124	1.45	P	16	4	0.227	1.41	P	663	988	0.01
332	*Symphurus* sp.	3.4	NA	1	0	0	-0.32	P	2	3	0	-0.35	P	0	1042	0
333	Synodontidae	4.3	NA	1	6	0	-0.56	P	1	0	0	-0.58	P	0	1354	0
334	Tellinidae	2.15	NA	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
335	Terebellidae	2.65	NA	3	2	0.444	-0.56	P	3	4	0.444	-0.54	P	16	1294	0
336	Terebridae	3.06	NA	2	1	0.5	-0.56	P	2	6	0.5	-0.58	P	23	1151	0
339	Thalassinidea	3.43	NA	1	2	0	-0.73	P	1	4	0	-0.70	P	0	1304	0
340	*Thalassoma lucasanum*	3.5	LC	1	0	0	-0.20	P	1	1	0	-0.20	P	0	1313	0
342	**Thunnus albacares*	4.41	NT	12	2	0.375	0.61	P	14	4	0.551	0.60	P	1590	983	0.01
344	*Trachypenaeus pacificus*	2.72	NE	2	1	0.5	-0.56	P	2	6	0.5	-0.58	P	0	1189	0
347	Trichuridae	4.5	NA	1	6	0	-0.56	P	1	0	0	-0.58	P	0	1354	0
346	*Trichiurus lepturus*	4.49	NE	1	0	0	-0.32	P	1	3	0	-0.57	P	0	1313	0
348	*Trinectes fonsecensis*	3.1-3.4	NE	5	1	0.32	-0.23	P	6	6	0.5	-0.21	P	169	1051	0
337	Triplasia	2.21	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
350	Triposolenia	1	NA	4	4	0	-0.27	P	4	5	0	-0.30	P	1	1197	0
351	*Ucides occidentalis*	2.6	NE	1	3	0	-0.31	P	1	8	0	-0.51	P	0	1178	0
352	**Urotrygon aspidura*	3.73	LC	7	6	0.612	-0.17	**P**	9	0	0.716	-0.35	**C**	39	960	0
354	*Urotrygon* spp.	3.8	NA	3	6	0.444	-0.33	**P**	4	3	0.625	-0.36	**C**	33	945	0
356	*Xiphopenaeus kroyeri*	2.7	NE	3	2	0	-0.39	P	4	4	0.375	-0.38	P	9	993	0
357	*Xiphopenaeus riveti*	3.31	NE	5	6	0.56	-0.17	P	7	8	0.571	-0.06	P	73	924	0
359	**Zapteryx xyster*	3.6	DD	6	6	0.278	0.16	P	6	8	0	0.25	P	43	1128	0
360	Zooplankton	2.21	NA	8	4	0.531	-0.15	P	8	5	0.594	-0.30	P	69	1119	0

Table S2. Changes in the structure of the food web with fisheries after simulations of species extinctions and fishery regulation. The percentage of species playing each topological role after a given extinction event is indicated as (%), M=Modularity, D= Degree, #M= number of modules, NH= Network hub, MH= Module hub, C= Connector, P= Peripheral. **P* <0.001.

Topological role	**Excluded node**	**M**	**D**	**#M**	**(%)**			
					NH	**MH**	**C**	**P**
Network hubs	*Sphyrna lewini*	0.49*	65	8	2,02	3,18	10,69	84,10
	Achirus klunzingeri	0.48*	21	8	1,11	3,61	9,72	85,56
Module hubs	*Lutjanus peru*	0.48*	21	8	1,42	3,12	11,05	84,42
	Mustelus lunulatus	0.49*	60	8	1,17	3,79	10,20	84,84
	Penaeus vannamei	0.49*	38	8	2,22	2,22	15,00	80,56
Connectors	*Katsuwonus pelamis*	0.48*	16	9	1,40	3,93	10,96	83,71
	Hypanus longus	0.49*	17	7	1,40	3,91	12,01	82,68
	Cetengraulis mysticetus	0.48*	12	8	1,11	3,60	10,53	84,76
Peripherals	*Thunnus albacares*	0.48*	14	8	1,12	3,64	11,20	84,03
	Cynoscion phoxocephalus	0.48*	11	8	1,67	3,06	10,00	85,28
	Rimapenaeus byrdi	0.47*	3	9	1,39	3,60	11,36	83,66
All	All nodes selected	0.49*	-	8	0,69	4,14	7,59	87,59
	Shrimp fisheries	0.48*	-	7	1,93	3,31	10,50	84,25
Network Hub-Connector	SSF-LSF	0.51*	66-39	7	1,11	3,33	10,28	85,28

Table S3. Species with varying trophic levels and topological roles whose extinctions were simulated in this study.

	Network hubs	Module hubs	Connectors	Peripherals
Low trophic level		*Penaeus vannamei*	*Cetengraulis mysticetus*	*Rimapenaeus byrdi*
Intermediate trophic level	*Achirus klunzingeri*	*Mustelus lunulatus*	*Hypanus longus*	*Cynoscion phoxocephalus*
High trophic level	*Sphyrna lewini*	*Lutjanus peru*	*Katsuwonus pelamis*	*Thunnus albacares*

TABLE S4. Changes in topological roles under the extinction and fishery regulations scenarios simulated in this study. Topological roles (TR; P: Peripherals, NH: Network hubs, MH: Module hubs, C: Connectors). Excluded nodes**:** Slew: *Sphyrna lewini*, Aklu: *Achirus klunzingeri*, Lpe: *Lutjanus peru*, Mlu: *Mustelus lunulatus*, Lva: *Litopenaeus vannamei*, Kpe: *Katsuwonus pelamis,* Hlo: *Hypanus longus*, Cmy: *Cetengraulis mysticetus*, Tal: *Thunnus albacares*, Cph*: Cynoscion phoxocephalus,* Rby: *Rimapenaeus byrdi,* Swsf: shallow-water shrimp fisheries, SSF: small-scale fisheries, LSF: large-scale fisheries.

								Excluded nodes							
Node	**Trophic component**	Slew	Aklu	Lpe	Mlu	Lva	Kpe	Hlo	Cmy	Tal	Cph	Rby	Swsf	All nodes	SSF-LSF
6	*Achirus klunzingeri*	NH	P	MH	MH	NH	MH	NH	NH	NH	NH	NH	C	P	MH
307	**Sphyrna corona*	NH	NH	NH	NH	NH	NH	NH	NH	MH	NH	MH	NH	MH	NH
308	*Sphyrna media*	NH	NH	NH	NH	NH	NH	NH	C	NH	NH	NH	C	MH	NH
361	SSF	NH	NH	NH	NH	NH	NH	NH	NH	NH	NH	NH	NH	NH	NH
362	LSF	NH	C	C	C	NH	C	C	C	MH	NH	C	C	C	P
195	**Mustelus henlei*	NH	MH	NH	MH	NH	MH	MH	MH	C	MH	MH	MH	MH	NH
309	*Sphyrna tiburo*	NH	MH	MH	MH	C	P	MH	C	C	C	P	MH	MH	NH
306	**Sphyrna lewini*		NH	NH	NH	NH	NH	NH	NH	NH	NH	NH	NH		NH
194	**Mustelus lunulatus*	MH	MH	MH		NH	MH	MH	MH	MH	MH	MH	MH		MH
60	*Cathorops manglarensis*	MH	MH	P	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH
87	*Cyclopsetta querna*	MH	MH	MH	MH	P	MH	MH	MH	P	P	MH	MH	MH	MH
245	*Litopenaeus stylirostris*	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH
246	**Litopenaeus vannamei*	MH	MH	MH	MH	P	MH	MH	MH	MH	MH	MH	MH		MH
176	**Lutjanus guttatus*	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH
207	*Notarius troschelii*	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH
222	*Ophioscion strabo*	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH
242	*Penaeus californiensis*	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH	MH
243	**Penaeus*	MH	MH	M	MH	M	MH	MH	MH	M	MH	MH	MH	MH	MH

	occidentalis			H		H				H					
353	**Urotrygon rogersi*	MH	MH	P	P	MH	NH	MH	P	MH	P	MH	MH	NH	NH
11	Algae	C	C	C	C	C	C	C	C	C	C	C	C	C	C
17	*Anchoa* spp.	C	P	C	P	C	P	C	C	C	C	C	P	C	C
31	*Bagre panamensis*	C	C	C	P	C	C	C	P	P	P	C	P	C	C
44	**Brotula clarkae*	C	P	C	C	C	C	C	C	C	P	C	C	P	C
46	Calappidae	C	C	C	P	C	C	C	P	C	C	C	C	C	C
52	Crabs	C	P	P	P	C	C	P	C	C	C	P	C	P	C
84	Crustaceans	C	C	C	C	C	C	C	C	C	C	C	C	C	C
151	Hippidae	C	P	P	P	P	P	P	P	P	P	P	P	P	P
315	*Michalisquilla parva*	C	P	P	P	P	P	C	P	C	C	C	C	P	C
230	Palaemonidae	C	P	C	P	C	C	C	C	C	C	P	P	P	C
241	Penaeidae	C	C	C	C	C	C	C	C	C	C	C	C	C	C
244	*Penaeus* spp.	C	P	P	P	C	P	P	P	C	C	P	P	P	C
253	Pleuronectiformes	C	C	C	C	C	C	C	C	C	C	C	C	P	C
264	Portunidae	C	P	C	C	C	C	C	P	C	P	C	P	P	C
266	*Portunus* spp.	C	P	C	C	C	C	C	C	C	C	C	C	P	C
273	*Protrachypene precipua*	C	C	C	C	P	C	C	P	P	P	C	C	C	C
274	*Pseudupeneus grandisquamis*	C	C	C	C	P	P	C	C	C	C	P	P	C	P
50	Shrimps	C	P	P	P	C	C	P	C	C	C	P	C	P	C
317	Squillidae	C	C	C	C	C	C	C	C	C	C	C	C	C	C
109	Stomatopods	C	P	C	P	C	P	C	C	C	C	C	C	P	C
355	Xanthidae	C	P	C	P	C	C	C	P	C	P	C	P	P	C
7	*Achirus mazatlanus*	C	C	C	C	C	P	P	C	P	C	C	C	C	P
123	Calappidae	P	P	P	P	P	P	P	P		P	P	P		P
55	**Caranx caninus*	C	C	C	C	C	C	C	C	C	C	C	C	C	P
57	*Carcharhinus leucas*	C	C	P	P	C	P	P	P	P	P	P	P	P	C
78	Clupeiformes	C	C	C	C	C	C	P	C	C	C	C	P	C	P
93	Dendrobranchiata	C	P	P	P	C	P	P	P	C	P	P	P	P	C
112	*Eugerres brevimanus*	C	C	C	C	C	C	C	C	C	C	C	C	P	C
220	Ophichthidae	C	P	P	C	C	P	C	P	C	P	C	C	P	C
254	Polychaeta	C	C	P	P	C	P	C	P	C	P	C	C	P	P
283	*Rimapenaeus byrdi*	C	P	P	P	P	P	P	P	P	P	P	P	P	C
287	*Rimapenaeus* spp.	C	P	P	P	P	P	P	P	P	P	P	C	P	C
289	Sciaenidae	C	C	C	C	C	C	C	C	C	C	P	P	C	C
303	*Sphoeroides annulatus*	C	C	C	C	C	C	C	C	C	C	C	C	C	C
312	*Squilla biformis*	C	P	P	P	P	P	P	P	P	P	P	P	P	C
352	**Urotrygon aspidura*	C	C	C	C	C	C	C	C	P	C	C	C	C	C
356	*Xiphopenaeus kroyeri*	C	P	P	P	P	P	P	P	P	P	P	P	P	P
177	**Lutjanus peru*	P	P	P	P	P	MH		MH	P	P	P	MH		MH
198	**Narcine leoparda*	P	P	P	MH	P	MH	MH	MH	MH	MH	NH	P	P	P

47	*Callinectes arcuatus*	P	C	C	C	C	C	C	C	C	C	C	C	C	C
49	*Callinectes toxotes*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
64	**Cetengraulis mysticetus*	P	P	C	C	P	C	C	P	P	P	C	C	P	P
34	Batrachoididae	P	P	C	C	P	P	C	P	C	P	C	P	P	P
160	**Katsuwonus pelamis*	P	P	P	C	C	P	P	C	P	C	P	C	P	P
165	Leucosiidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
122	Phytoplankton	P	P	P	P	P	P	P	P	P	P	P	P	P	P
278	**Pseudobatos leucorhynchus*	P	P	C	P	C	C	C	P	C	C	P	P	P	C
299	*Solenocera agassizii*	P	P	P	P	C	P	P	C	P	P	P	C	P	P
301	Solenoceridae	P	P	P	P	C	P	P	P	P	C	P	P	P	P
313	*Squilla mantoidea*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
316	*Squilla* sp.	P	C	C	C	C	C	C	C	C	C	C	C	P	C
345	*Trachypenaeus* spp.	P	P	P	P	C	P	P	P	P	P	P	P	P	P
343	Turtles	P	P	P	P	P	P	P	P	P	P	P	P	P	P
358	*Xiphopenaeus* sp.	P	P	C	P	C	P	C	C	P	P	C	P	C	C
1	*Abraliopsis* spp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
2	Acanthochiasma	P	P	P	P	P	P	P	P	P	P	P	P	P	P
3	Acantholithium	P	P	P	P	P	P	P	P	P	P	P	P	P	P
4	Acanthometra	P	P	P	P	P	P	P	P	P	P	P	P	P	P
8	**Aetobatus narinari*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
9	Albuneidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
10	Alpheidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
12	*Alpheus* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
13	*Aluterus* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
14	*Ambidexter panamensis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
15	Amphipoda	P	P	P	P	P	P	P	P	P	P	P	P	P	P
18	*Anchovia macrolepidota*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
16	*Anchoa spinifer*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
19	*Anchoa starksi*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
20	Anguilliformes	P	P	P	P	P	P	P	P	P	P	P	P	P	P
21	*Anisotremus* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
22	Anomura	P	P	P	P	P	P	P	P	C	P	C	P	P	P
23	*Aratus pisonii*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
24	*Arenaeus mexicanus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
25	Ariidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
26	*Ariopsis seemanni*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
27	Ascidians	P	P	P	P	P	P	P	P	P	P	P	P	P	P
28	Astrolithidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
29	Aulopiformes	P	P	P	P	P	P	P	P	P	P	P	P	P	P
30	Axiidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
32	Balistidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
33	*Bathygobius* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P

35	Batoidea	P	P	P	P	C	P	P	C	P	P	P	P	P	P
36	Beloniformes	P	P	P	P	P	P	P	P	P	P	P	P	P	P
37	*Benthesicymus tanneri*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
38	Biddulphia	P	P	P	P	P	P	P	P	P	P	P	P	P	P
39	Bivalves	P	C	P	P	C	C	C	P	C	P	C	P	P	P
40	*Bollmannia chlamydes*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
41	Bothidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
42	Brachyura	P	P	P	P	P	P	P	P	P	P	P	P	P	P
43	*Bregmaceros bathymaster*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
45	Buccinidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
48	*Callinectes* spp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
51	*Cancer johngarthi*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
53	Capitellidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
54	Carangidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
56	*Caranx* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
59	Carditidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
58	Caridea	P	P	P	P	P	P	P	P	P	P	P	P	P	P
86	Cavoliniidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
62	*Centropomus unionensis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
61	Cephalopods	P	P	P	P	P	P	P	P	C	P	P	C	P	C
63	Ceratium	P	P	P	P	P	P	P	P	P	P	P	P	P	P
65	Chaenopsidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
66	Chaetoceros	P	P	P	P	P	P	P	P	P	P	P	P	P	P
67	Chaetognats	P	P	P	P	P	P	P	P	P	P	P	P	P	P
68	*Chloroscombrus orqueta*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
69	*Chloroscombrus* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
70	*Chromis* spp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
71	Cyanobacterias	P	P	P	P	P	P	P	P	P	P	P	P	P	P
72	Cirratulidae	P	P	P	P	C	P	P	P	P	P	P	C	P	P
73	Cirripedians	P	P	P	P	P	P	P	P	P	P	P	P	P	P
74	*Citharichthys gilberti*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
75	Cladocerans	P	P	P	P	P	P	P	P	P	P	P	P	P	P
76	*Cloridopsis dubia*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
77	Clupeidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
79	Cnidarians	P	P	P	P	P	P	P	P	P	P	P	P	P	P
80	Congridae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
81	Copepods	P	P	P	P	P	P	P	P	P	P	P	P	P	P
82	Corallanidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
83	Coscinodiscus	P	P	P	P	P	P	P	P	P	P	P	P	P	P
85	Cumacea	P	P	P	P	P	P	P	P	P	P	P	P	P	P
341	Collodaria	P	P	P	P	P	P	P	P	P	P	P	P	P	P

89	Cynoglossidae	P	C	C	C	C	C	C	P	P	C	P	P	C	P
92	*Cynoscion analis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
90	**Cynoscion phoxocephalus*	P	P	C	C	P	C	P	P	P	P	C	C	P	P
91	*Cynoscion* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
199	Decapoda	P	P	P	P	P	P	P	P	P	P	P	P	P	P
338	Decapodiformes	P	P	P	P	C	P	P	C	C	C	P	P	P	C
94	Detritus	P	P	P	P	P	P	P	P	P	P	P	P	P	P
95	*Diapterus* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
96	Diatoms	P	P	P	P	P	P	P	P	P	P	P	P	P	P
97	Dinoflagellates	P	P	P	P	P	P	P	P	P	P	P	P	P	P
98	Diogenidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
99	*Diplectrum*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
100	Ditylum	P	P	P	P	P	P	P	P	P	P	P	P	P	P
101	Dorippidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
167	*Doryteuthis (Amerigo) gahi*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
102	*Dosidicus gigas*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
103	Drilonereis	P	P	P	P	P	P	P	P	P	P	P	P	P	P
108	Echinoderms	P	P	P	P	P	P	P	P	P	P	P	P	P	P
105	*Echiophis brunneus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
106	*Emerita* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
107	Engraulidae	P	P	P	P	C	P	C	P	P	P	P	P	P	P
110	*Ethusa ciliatifrons*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
111	*Eucinostomus* spp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
104	*Eugerres lineatus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
113	*Eunice* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
114	Eunicidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
115	Euphausiacea	P	P	P	P	P	P	P	P	P	P	P	P	P	P
116	*Euphylax robustus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
117	*Euphylax* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
118	*Eurypanopeus transversus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
119	Exocoetidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
164	Flatfishes	P	P	P	P	P	P	P	P	P	P	P	P	P	P
121	*Fistularia* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
124	Galatheidae	P	P	P	P	P	P	P	P	C	P	P	P	P	C
125	Gammaridea	P	P	P	P	P	P	P	P	P	P	P	P	P	P
126	Gastropoda	P	C	P	C	C	C	P	C	P	C	C	C	P	P
127	Gigartaconidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
128	Glycera	P	P	P	P	P	P	P	P	P	P	P	P	P	P
129	Glyceridae	P	P	P	P	P	P	P	C	P	C	P	P	C	P
130	Gobiidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
131	*Gonatus onyx*	P	P	P	P	P	P	P	P	P	P	P	P	P	P

132	Goneplacidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
133	Goniada	P	P	P	P	P	P	P	P	P	P	P	P	P	P
134	Goniadidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
135	*Goniadides* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
136	*Goniopsis pulchra*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
137	Gonodactylidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
138	Gonostomatidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
139	Grapsidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
140	*Grapsus grapsus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
141	*Guyanacaris caespitosa*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
142	*Gymnothorax equatorialis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
147	*Haemulopsis nitidus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
148	*Halichoeres aestuaricola*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
143	*Halichoeres chierchiae*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
144	*Halichoeres dispilus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
145	*Halichoeres notospilus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
146	*Harengula thrissina*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
149	*Hepatus kossmanni*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
150	*Hepatus* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
152	*Histioteuthis* cf. *heteropsis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
5	Holacanthida	P	P	P	P	P	P	P	P	P	P	P	P	P	P
153	*Hyaloteuthis pelagica*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
154	**Hypanus longus*	P	C	C	C	C	C	P	C	C	C	C	C	P	C
155	*Ichthyapus selachops*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
156	Ichthyoplankton	P	P	P	P	P	P	P	P	P	P	P	P	P	P
158	Inachoididae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
159	Isopoda	P	P	P	P	P	P	P	P	P	P	P	P	P	P
161	*Larimus argenteus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
162	*Larimus* spp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
163	*Leachia danae*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
166	*Lile stolifera*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
169	Loliginidae	P	C	C	C	C	C	C	P	P	C	P	P	P	P
168	*Loligo* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
170	*Lolliguncula argus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
171	*Lolliguncula diomedae*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
172	*Lolliguncula panamensis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
173	Luciferidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
174	Lumbrineridae	P	P	P	P	P	P	P	P	P	P	P	P	P	P

175	**Lutjanus argentiventris*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
178	*Lysiosquilla panamica*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
179	*Lysiosquilla* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
180	Lysiosquillidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
181	*Macrobrachium americanum*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
182	Macroalgae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
183	*Macrodon mordax*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
184	Majidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
185	*Meiosquilla dawsoni*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
186	Melosira	P	P	P	P	P	P	P	P	P	P	P	P	P	P
187	*Metapenaeopsis beebei*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
188	Mollusca	P	P	P	P	P	P	P	P	P	P	P	P	P	P
189	*Mugil curema*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
190	Mugilidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
191	Munida	P	P	P	P	P	P	P	P	P	P	P	P	P	P
192	*Munida obesa*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
193	*Muraena* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
196	*Myrophis vafer*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
197	Mysida	P	P	P	P	P	P	P	P	P	P	P	P	P	P
200	Navicula	P	P	P	P	P	P	P	P	P	P	P	P	P	P
201	Nemertea	P	P	P	P	P	P	P	P	P	P	P	P	P	P
202	*Neodoclea boneti*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
203	*Neogonodactylus stanschi*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
204	Nephtyidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
205	Nereididae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
206	Nereis	P	P	P	P	P	P	P	P	P	P	P	P	P	P
208	Nucula	P	P	P	P	P	P	P	P	P	P	P	P	P	P
209	*Ocypode* spp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
210	Oenonidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
211	Ogyrididae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
212	*Ogyrides alphaerostris*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
215	Oligochaeta	P	P	P	P	P	P	P	P	P	P	P	P	P	P
214	*Oligoplites refulgens*	P	C	P	P	P	C	P	P	P	P	P	P	C	P
213	*Oligoplites* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
216	Olividae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
217	*Ommastrephes bartramii*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
218	Onuphidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
219	*Onychoteuthis banksii*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
221	*Ophichthus frontalis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
223	*Opisthonema libertate*	P	P	P	P	P	P	P	P	P	P	P	P	P	P

224	*Opisthonema* spp.	P	P	P	P	P	P	P	P	C	P	C	P	P	P
225	*Opisthopterus* sp.	P	P	P	P	P	P	C	P	P	P	P	P	P	P
226	Ostracoda	P	P	P	P	P	P	P	P	P	P	P	P	P	P
227	*Pachygrapsus transversus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
229	*Palaemon* sp.	P	C	P	P	P	P	P	P	P	P	P	P	P	P
228	Palicidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
232	Pandalidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
233	*Panopeus purpureus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
234	*Paradasygyius depressus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
236	Paralichthyidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
235	*Paralonchurus petersii*	P	C	C	C	C	C	C	C	P	P	C	P	P	P
237	*Parasquilla similis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
238	*Parthenope* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
239	Pasiphaeidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
240	Pectinariidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
120	*Penaeus brevirostris*	P	C	C	C	C	C	C	C	P	P	C	P	P	P
247	Perciformes	P	P	P	P	P	P	P	P	P	P	P	P	P	P
248	Peridinium	P	P	P	P	P	P	P	P	P	P	P	P	P	P
157	*Persephona subovata*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
249	*Petrolisthes zacae*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
250	Phyllodocidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
251	Phyllostauros	P	P	P	P	P	P	P	P	P	P	P	P	P	P
252	Pinnotheridae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
349	Plagiacantha	P	P	P	P	P	P	P	P	P	P	P	P	P	P
231	Pleocyemata	P	P	P	P	P	P	P	P	P	P	P	P	P	P
255	*Polydactylus approximans*	P	C	P	C	P	C	C	P	P	C	C	P	C	P
256	*Polydactylus opercularis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
257	Polynemidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
258	Polyplacophora	P	P	P	P	P	P	P	P	P	P	P	P	P	P
259	Polystira	P	P	P	P	P	P	P	P	P	P	P	P	P	P
260	*Pomadasys panamensis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
261	Porcellanidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
262	*Porichthys margaritatus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
263	*Porichthys* spp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
265	*Portunus asper*	P	C	P	P	C	P	P	P	P	P	P	P	P	P
267	*Portunus xantusii*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
268	*Prionotus horrens*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
269	Pristigasteridae	P	P	P	P	P	P	P	P	P	P	P	P	P	P

270	*Processa peruviana*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
271	*Processa* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
272	Processidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
275	Pseudosquillidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
276	Pteropoda	P	P	P	P	P	P	P	P	P	P	P	P	P	P
277	Pycnogonidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
279	*Raja velezi*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
88	Ranellidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
281	Raninidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
280	*Raninoides benedicti*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
282	Rhizosolenia	P	P	P	P	P	P	P	P	P	P	P	P	P	P
284	*Rimapenaeus faoe*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
285	*Rimapenaeus fuscina*	P	C	C	C	C	C	C	C	P	P	C	C	P	P
286	*Rimapenaeus pacificus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
290	**Scomberomorus sierra*	P	P	P	P	P	P	C	P	P	P	P	P	P	P
291	Scombridae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
292	Scorpaeniformes	P	P	P	P	P	P	P	P	P	P	P	P	P	P
293	Scyphozoa	P	P	P	P	P	P	P	P	P	P	P	P	P	P
294	**Selene peruviana*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
296	*Sesarma rhizophorae*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
295	*Sergia inoa*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
328	*Sicyonia disdorsalis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
297	*Sicyonia picta*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
329	*Sicyonia* sp.	P	C	C	C	C	C	C	C	C	C	C	C	P	C
330	Sicyoniidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
298	Sipuncula	P	P	P	P	P	P	P	P	P	P	P	P	P	P
288	*Skeletonema*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
300	*Solenocera* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
302	Sphaerozoum	P	P	P	P	P	P	P	P	P	P	P	P	P	P
304	*Sphyraena* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
305	Sphyraenidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
310	Spionidae	P	P	P	P	C	P	P	P	P	P	P	C	P	P
311	*Squilla aculeata*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
314	*Squilla panamensis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
318	*Stellifer fuerthii*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
319	*Stellifer melanocheir*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
320	*Stellifer oscitans*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
321	*Stellifer* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
322	*Stellifer zestocarus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
323	*Stenocionops ovatus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
324	*Stenorhynchus debilis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
325	Sternaspidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P

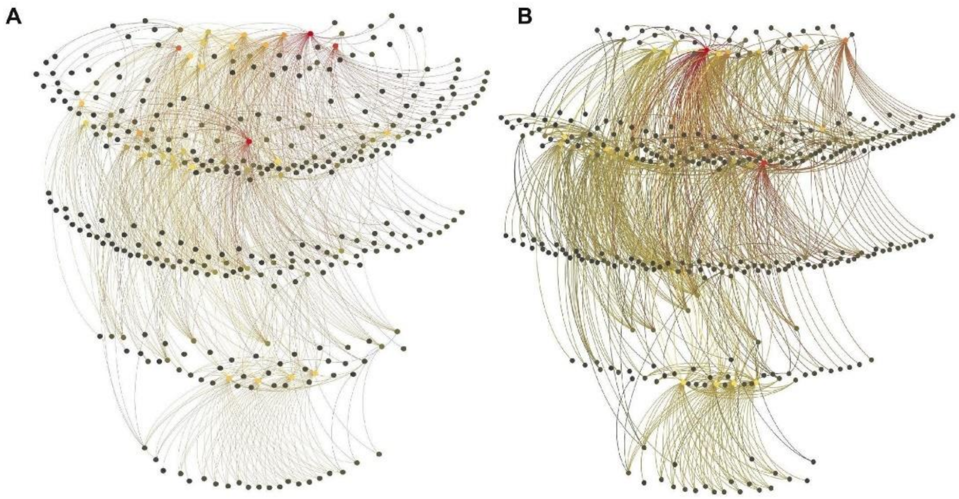
326	*Sthenoteuthis oualaniensis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
327	*Strongylura* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
331	*Symphurus elongatus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
332	*Symphurus* sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
333	Synodontidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
334	Tellinidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
335	Terebellidae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
336	Terebridae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
339	Thalassinidea	P	P	P	P	P	P	P	P	P	P	P	P	P	P
340	*Thalassoma lucasanum*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
342	**Thunnus albacares*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
344	*Trachypenaeus pacificus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
347	Trichuridae	P	P	P	P	P	P	P	P	P	P	P	P	P	P
346	*Trichiurus lepturus*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
348	*Trinectes fonsecensis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
337	Triplasia	P	P	P	P	P	P	P	P	P	P	P	P	P	P
350	Triposolenia	P	P	P	P	P	P	P	P	P	P	P	P	P	P
351	*Ucides occidentalis*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
354	*Urotrygon* spp.	P	C	C	C	C	C	C	C	P	P	C	P	P	P
357	*Xiphopenaeus riveti*	P	P	P	P	C	P	P	P	P	P	P	P	P	P
359	**Zapteryx xyster*	P	P	P	P	P	P	P	P	P	P	P	P	P	P
360	Zooplankton	P	P	P	P	P	P	P	P	P	P	P	P	P	P

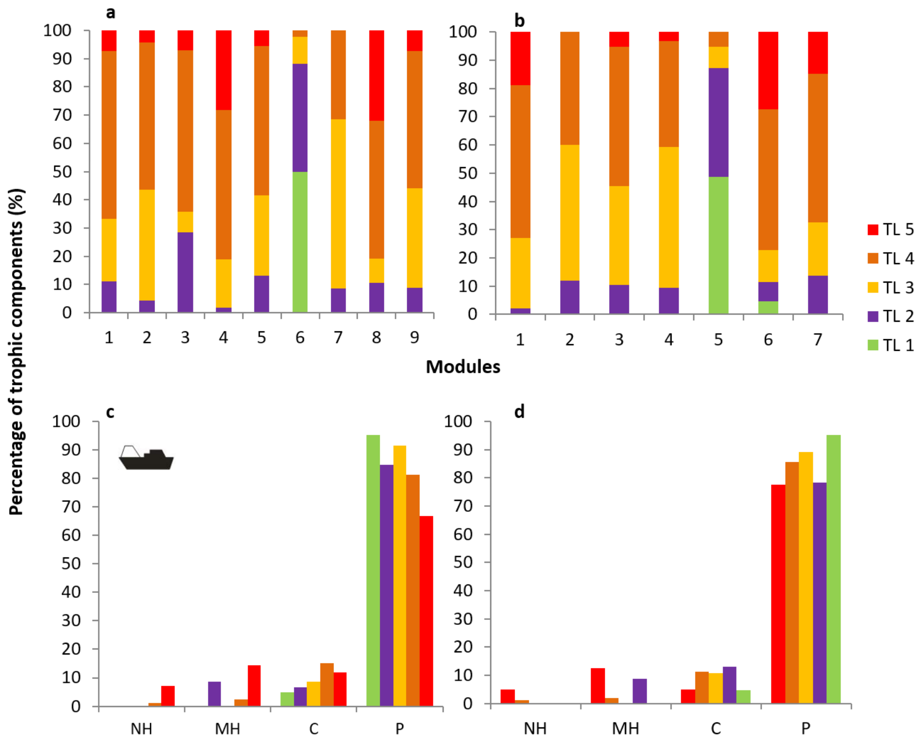
FIGURE LEGENDS

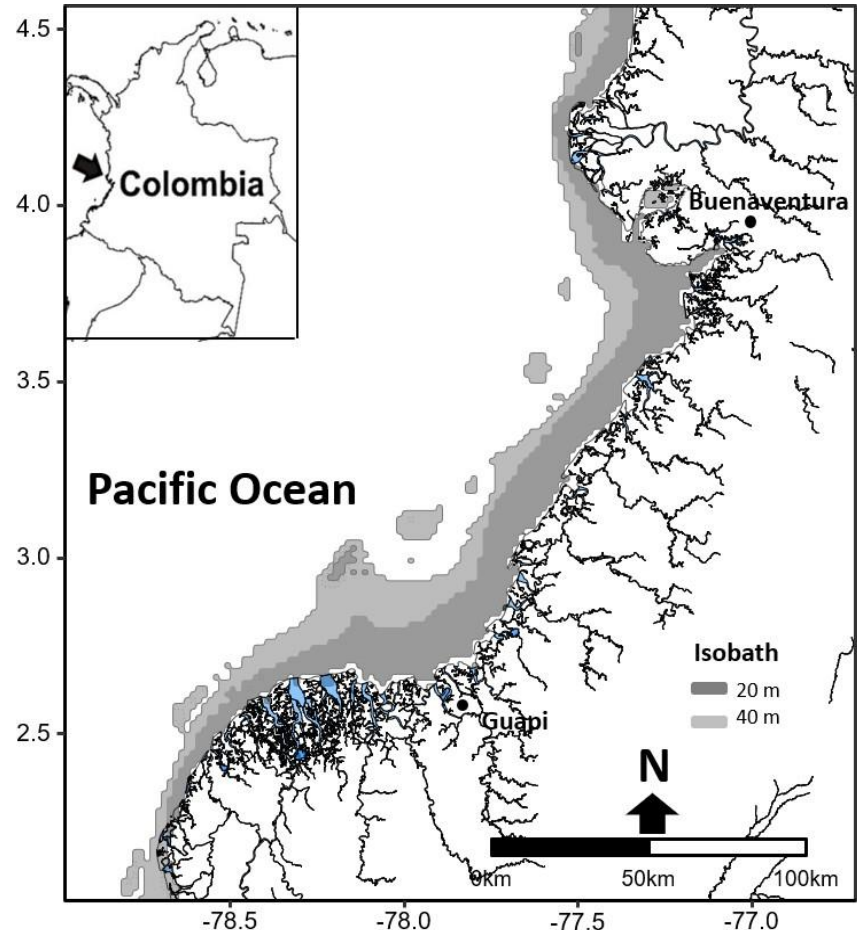
FIGURE S1. The modular structure of the coastal food web in the central-south Colombian Pacific coast. The colors of the nodes and links vary according to within-Module degree (*z*) values in (*A*) the food web including fisheries and (*B*) the food web without fisheries. In the temperature scale used, cold and hot colors indicate, respectively, low and high *z* values.

FIGURE S2. Distributions of species from different trophic levels according to network modules (*A*, *B*) and frequency of species playing each topological and their respective trophic levels (*C*, *D*) The panels *A* and *C* refer to the food web including fisheries as nodes and the panels *B* and *D* refer to the food web without fisheries. role NH: Network hubs, MH: Module hubs, C: Connectors, P: Peripherals.

FIGURE S3. The study area in the Colombian Pacific coast showing the isobaths of small-scale fisheries (20 m) and large-scale fisheries (40 m).


A
B


a
b
c
d
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
Modules
Percentage of trophic components (%)
TL 5
TL 4
TL 3
TL 2
TL 1
NH
MH
C
P


4.5
4.0
3.5
3.0
2.5
-78.5
-78.0
-77.5
-77.0
Colombia
Pacific Ocean
Buenaventura
Guapi
Isobath
20 m
40 m
N
0km
50km
100km

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CHAPTER III

Capítulo a ser submetido para a publicação na revista *Ecological Modelling*.

Ecological dynamics of an anthropogenic coastal marine food webs

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Formatado de acordo com as normas da Ecological modelling

Abstract

Interspecific interactions are major drivers of the structure and stability of communities. Changes in interaction patterns over time in response to environmental and anthropogenic shifts influence not only biodiversity patterns, but also the functioning of marine ecosystems. During the last decade, contrasting results have been obtained on rewiring of interactions in food webs as a mechanism of population stabilization within communities. We studied the ecological dynamics of an anthropogenic coastal food web in the Pacific Ocean that encompasses 360 species and small- and large-scale fisheries. We modelled the dynamic of a food web in terms of abundances of species over time, to explore the consequences of rewiring trophic interactions. The coastal food web undergoes a substantial change in abundances of species in all the scenarios of fishery pressure, affecting all trophic levels, with high extinction fractions mainly of top predators, and with a strong negative effect on resilience. Thus, the rewiring of interactions has a strong influence in the dynamic response of the food web, with long-term negative effects, which can lead to the collapse of the network. The inclusion of rewiring of interactions in dynamic models of ecological networks is an essential component to explore, understand and foresee the responses of marine ecosystems to anthropogenic activities, aiming at maintenance of biodiversity and ecosystem services of coastal marine areas.

Keywords: coastal marine food web, artisanal fisheries, rewiring of interactions, forbidden links, community stability, resilience, adaptive networks

Introduction

Rapid changes in biodiversity patterns due to ocean warming, overfishing and several other anthropogenic impacts is a marked feature of the Anthropocene (Hilborn et al., 2004; Barnosky, 2011; McCauley et al., 2015; Johnson et al., 2017). Anthropogenic processes became key drivers of ecological and evolutionary dynamics of populations and communities (Palkovacs, 2011; Norberg et al., 2012; Palkovacs et al., 2012; Hendry et al., 2017; Perälä & Kuparinen, 2020). Overfishing is one of the main anthropogenic disturbances that jeopardize ecosystems services, as food provision and employment for many human communities around the world (FAO, 2018, 2020). Therefore, understanding how anthropogenic changes in marine ecosystems reshape local patterns of ecological interactions is key to conserving and promoting the sustainable use of marine ecosystems, in line with the United Nations sustainable development goals marine resources (SDG14, https://sustainabledevelopment.un.org).

Research over the last few decades has shown that fishing activities may impose ecological changes in marine ecosystems, by modifying community compositions, triggering the evolution of body sizes within populations (Baum and Worm, 2009; Pauly et al., 1998), causing the loss of genetic diversity within species (Pinsky and Palumbi, 2014) and promoting pervasive structural changes within food webs (Bascompte et al., 2005; Gaichas and Francis, 2008; Chen et al., 2016; Navia, et al., 2012). Regarding the latter point, species trophic interactions vary widely in space and time, implying corresponding variations in the dynamics of local communities (Berlow, 1999; Navarrete and Berlow, 2006; Valdovinos et al., 2010; Ushio et al., 2018).

Fishing can influence interaction patterns due to the addition or loss of pairwise throphic interactions as a consequence of adaptive or stochastic processes - *rewiring*- (Thierry et al., 2011; Bartley et al., 2019). Interaction rewiring arising from species loss are expected to rebalance the network back to its demographic equilibrium, buffering ecosystems against environmental or anthropogenic perturbations (Kondoh, 2003; Staniczenko et al., 2010; Nuwagaba et al., 2015). Although it has been suggested that rewiring should be advantageous for individual predators in the short term (Staniczenko et al., 2010), it may be damaging for the long-term system persistence (Gilljam et al., 2015). On one side, the ability of consumers to switch interactions to explore novel prey should mitigate the consequences of species loss by reducing the risk of cascading extinction (Staniczenko et al., 2010). Conversely, it may represent an additional perturbation to the network since a rewired predator species turns into a native invader (Carey et al., 2012) by increasing the overexploitation of the remaining prey species (Brashares et al., 2004; Newsome et al., 2010; Prop et al., 2015).

The rewiring of interactions considering the feedback between node properties and network topology, has been suggested a key force that shape the structure of ecological networks (Suweis et al., 2013; Raimundo et al., 2018). Studies about the direct and indirect effects of rewiring on the structure and dynamics of food webs following environmental and anthropogenic disturbances are an important aspect for conservation of marine biodiversity and the management of resources, which is gradually being explored (e.g., Staniczenko et al., 2010; Thierry et al., 2011; Blanchard, 2015; Gilljam et al., 2015; Ushio et al., 2018; Bartley et al., 2019; D´Alelio et al., 2019). For instance, it has been shown that highly mobile generalist fish species are switching their trophic interactions as they colonize novel marine regions where they were previously absent due to climate changes, promoting a generalized rewiring of marine food webs (Blanchard, 2015; Kortsch et al., 2015; Bartley et al., 2019; Pecuchet et al., 2020), while keeping almost the same global flow to upper trophic levels (D´Alelio et al., 2019).

Several mechanisms have been proposed to explain the interaction patterns of food webs, which can influence the rewiring. The reciprocal effects between trait-based (Cohen et al., 2003; Laigle et al., 2018; Rezende et al., 2009) and neutral processes (Cohen et al., 2003; Vásquez et al., 2007) form a feedback loop between ecological and evolutionary dynamics, which dynamically connect interaction patterns, community stability and functional diversity (see Raimundo et al., 2018 and references therein; Segar et al., 2020). In this context, the adaptive network models are a promising tool that can be useful to provide predictions of how community properties will change over time in response to the interplay between interaction rewiring, species abundances and traits (Gross and Blasius, 2008; Gross and Sayama, 2009; Suweis et al., 2013; Poisot et al., 2015).

Dynamic network models incorporating interaction rewiring can help us to predict, for example, how improved fisheries regulations may promote competition releases and change the interaction patterns of key central species, which may have broader structural and dynamical consequences for marine food webs (Thierry et al., 2011). Additionally, this integrative framework can allow the systematic investigation of how multiple structural alternatives may fulfill the conditions for species coexistence and for the stability of the ecological networks (Rohr et al., 2014; Staniczenko et al., 2010; Allesina and Tang, 2015; Andreazzi et al., 2018). These dynamic models have been recently proposed as a tool for biodiversity conservation and restoration (Raimundo et al., 2018; Valdovinos et al., 2019) and could greatly improve our understanding and ability to predict the effect at community level of anthropogenic disturbances and to advance in the management of marine ecosystems aiming the maintenance of biodiversity and ecosystem services.

The goal of this work is to explore the implication of the rewiring of trophic interactions by fisheries-induced species losses for the dynamics of a coastal marine food web in the Tropical Pacific Ocean. In doing so, we aimed to: (1) develop an adaptive network model that describe the ecological dynamic of the food web using empirical trophic and fisheries data; (2) assess how the rewiring of interactions influence the persistence of species (proportion of species surviving in a given period) and resilience of food web (3) How different scenarios of fishery pressure influence the dynamic response of the food web.

Materials and methods

Food web data

We analysed a food web depicting the trophic interactions of a marine ecosystem in the central-south coast of Colombia (see Márquez-Velásquez et al., 2021). The network has a modular structure and encompasses 360 species. We also considered as nodes within the network two human agents, namely small- scale (SSF) and large-scale fisheries (LSF). Their catches were also included as additional links in the network. Small-scale (artisanal) fisheries nodes encompass bottom trawls used by shallow-water shrimp fisheries, hand lines, longlines, gillnets and beach seines. The large-scale (industrial) fisheries node refers exclusively to deep-water shrimp fisheries (Gallardo et al., 2018). The dataset includes information on resource use that encompasses detritus, phytoplankton, zooplankton, invertebrates, turtles, elasmobranchs, and bony fishes. Details on how the food web was assembled, on habitat and fisheries characteristics are discussed elsewhere (Navia et al., 2016; Márquez-Velásquez et al., 2021).

The Marine Food Web Model

To model the ecological dynamics of the marine food web, we combined a model of population dynamics with the rewiring of ecological interactions. Our modelling approach consisted of three main steps. First, we numerically simulated the population dynamics of the food web until an equilibrium was reached. Second, we applied a rewiring algorithm using the abundance of each species at the equilibrium. Third, we repeated steps one and two until the structure of the food web reached asymptotic values.

Modelling population dynamics

We modelled the population dynamics of each species *i* of the food web using a classical food web model with Holling type II functional response:

$$\frac{dN_i}{dt} = N_i\left(r_i - \gamma_i N_i - \sum_{j=1}^{N}\frac{v_{ij}N_j}{1 + h_j v_{ij} N_j} + \sum_{j=1}^{N}\frac{p_{ij}N_j}{1 + h_i p_{ij} N_j}\right) \tag{1}$$

where N_i corresponds to species abundance or biomass, r_i is the intrinsic growth rate, γ_i the coefficient of intraspecific competition, $h_i(h_j)$ is the handling time, v_{ij} is the effect of species *j* as a predator of *i*, and p_{ij} is the effect of species *i* as a predator of *j*. The intrinsic growth rate of species, r_i, is a function of the species births, b_i and species deaths from fishery activity, d_i. We assumed that species births decays with the body size, z_i, of the species:

$$b_i = e^{-z_i{}^2} \tag{2}$$

For species deaths from fishery pressure, we assumed that the larger the body size of the species in respect to the gill sizes of bottom trawls (θ), the larger the effect of fishery on the species:

$$d_i = \frac{1}{1 + e^{-\beta(z_i - \theta_i)}} \tag{3}$$

where β is a parameter that controls how sensitive species deaths are in respect to the differences between species body size (z_i) and the gill sizes of bottom trawls of the ship (θ).

Furthermore, in our model we assumed that the effects of a predator j on a prey i (v_{ij}) and vice-versa (p_{ij}) are sigmoid functions of the body sizes of the predator and the prey:

$$v_{ij} = a_{ij} \frac{1}{1 + e^{-\alpha(z_j - z_i)}} \tag{4}$$

$$p_{ij} = a_{ji} \frac{1}{1 + e^{-\alpha(z_i - z_j)}} \tag{5}$$

where $a_{ij} = 1$ if species *i* is a prey of species *j* or $a_{ij} = 0$ otherwise, $a_{ji} = 1$ if species *i* is a predator of species *j* and $a_{ji} = 0$ otherwise, and α is a parameter that controls how sensitive v_{ij} and p_{ij} are to differences between species body sizes (z_i and z_j). Thus, the larger the body size of a predator *j* in respect to a prey *i*, the larger its effect as a predator of *i* and the closer v_{ij} is to the function maximum value ($0 < v_{ij} < 1$). Similarly, the larger the body size of a predator *i* in respect to a prey *j*, the larger the effect of *i* as a prey of *j* and p_{ij} approaches its máximum value ($0 < p_{ij} < 1$).

We parameterized the functions described by equations 3-5 using empirical data available for the maximum body sizes (z) of the species in the marine food web, and for the gill sizes of bottom trawls used by shallow-water shrimp fisheries in the study area (θ=5cm). We used the maximum body size of the species of the marine food web because it is long been known to play an important role in determining predator-prey interactions through gape limitation in aquatic food webs (Arim et al., 2010, Schneider et al., 2012; Kalinkat et al., 2013; DeLong et al., 2015). All empirical data on max body size for the 360 species of the food web was obtained from the databases Fish Base (Froese & Pauly, 2020) and Sea Around Us (www.seaaroundus.org). The system of differential equations specified by equations 1-5 were numerically solved using the package DifferentialEquations of the Julia programming language v 1.6.0 (Bezanson et al., 2017).

Interaction rewiring

After the ecological dynamics reached an equilibrium, all species in the food web had the opportunity to rewire their interactions. Our rewiring algorithm followed two steps. First, each species *i* had a probability to rewire their interactions. This probability was proportional the ratio of the total abundance of all resource species *j* consumed by species *i*, in respect to the total abundance of species in the food web:

$$P(Rewiring) = 1 - \frac{\sum_{j=1}^{N} a_{ji} N_j^*}{\sum_{k=1}^{N} N_k^*} \tag{6}$$

where $N_j^*(N_k^*)$ corresponds the equilibrium species abundance. Therefore, the smaller the abundance of the preys of species *i* in respect to the total abundance of species in the food web, the larger the probability of species *i* to rewire its interactions. Second, if species *i* undergo rewiring of interactions, we assumed that it could prey on any other species *j* in the food web with probability that depends on the abundance of species *j* in respect to all other species in the food webs, and on the differences of the body sizes between species *i* and *j:*

$$P\left(a_{ji} = 1\right) = f_{ij} \frac{N_j^*}{\sum_{k=1}^{N} N_k^*} \frac{1}{1 + e^{-\alpha\left(z_i - z_j\right)}} \tag{7}$$

where f_{ij} is a parameter that controls whether species *i* can prey on species *j*, e.g., it controls forbidden links in the food web. When $f_{ij} = 0$, there is a forbidden link that prohibits species *i* to prey on species *j*, and $f_{ij} = 1$ otherwise. Forbidden links limits the extent to which the network structure can change, since most food resources may not be accessible to most species (Olesen et al., 2011; Stouffer et al., 2011; Woodward et al., 2005). We determined the forbidden links considering restrictions on habit use, feeding strategies and body size between interacting pairs of species, using data from the literature and the databases *Fish Base* (Froese and Pauly, 2018) and *Sea Around Us* (www.seaaroundus.org). Thus, if there is not a forbidden link, the larger the abundance of species *j* and the larger the difference between the body sizes of *i* and *j*, the larger the probability that species *i* rewire its interactions to prey on species *j*. The rewiring algorithm was implemented using the Julia programming language v1.6.0 (Bezanson et al., 2017).

Food web resilience.

We calculated the resilience of the food web with and without rewiring, defined as the ability of a complex system to withstand perturbation and avoid switching from a relatively high to much lower mean value of a focal state variable (Gao et al., 2016). The resilience function is calculated as:

$$\beta_{\mathrm{eff}} = \langle s \rangle + SH,$$

where $\langle s \rangle$ is the network density measured as the average edge weight; $H= \sigma_{\mathrm{in}}\mathrm{o}_{\mathrm{ut}}/\langle s \rangle$ is the heterogeneity in the weighted degrees s^{in} and s^{out}, being σ^2_{in} and σ^2_{out} the variance of the marginal probability density functions $P(s^{\mathrm{in}})$ and $P(s^{\mathrm{out}})$ respectively. Finally, $S= (\langle s^{\mathrm{in}}s^{\mathrm{out}} \rangle - \langle s^{\mathrm{in}} \rangle \langle s^{\mathrm{out}} \rangle)/(\sigma_{\mathrm{in}}\sigma_{\mathrm{out}})$ is the symmetry between s^{in} and s^{out}, which are the vector of in–out weighted-degree correlation coefficient. In terms of vulnerability, this resilience metric is directly related to the sensitivity of marine food web to perturbation.

The model was carried out for three scenarios of fishery pressure, considering three different gill sizes of bottom trawls of the ship (θ).: (θ)=0, medium (θ=0.5) and high (θ=1). For each scenario were performed 100 simulations of rewiring events (Table 1). In each scenario was calculated the resilience, average species abundances and fraction of species extinct.

Table 1. List of variables and parameter values used in the model

Notation	Definition	Value
zi, zj	Body size	Provided by a data base
rij	The intrinsic growth rate	Is a function of the species births (bi) and species deaths from fishery activity (di)
bi	Species births, decaying with the body size	e^(-zi^2)
*d*i	Mortality due to fishing (θ)	θ=0, θ=0.5, θ=1
ϒi	The coefficient of intraspecific competition	1
*h*i	The handling time	0.5
vij	Is the effect of species j as a predator of i	A sigmoid function of the body sizes of the predator and the prey
pij	Is the effect of species i as a predator of j	A sigmoid function of the body sizes of the predator and the prey
Nj*(Nk*)	The equilibrium species abundance	Estimated from the data
fij	Is the matrix of forbidden links.	fij=0 there is a forbidden link that prohibits species *i* to prey on species *j*, and fij=1 otherwise

Results

In our models without fisheries, the main fraction of species extinct in the scenario encompassing rewiring events was lower (0.652 ± SD= 0.01) than in those without rewiring (0.720 ± 0.00) (Fig. 1). Under an intermediate fishery pressure, extinctions drastically increase for both scenarios – with and without interaction rewiring (0.840 ± 0.003; 0.831 ± 0.000). Such a trend is confirmed by the high fishing pressure scenario, under which extinctions reached maximum degrees (0.842 ± 0.0; 0.836 ± 0.0) (Fig. 1).

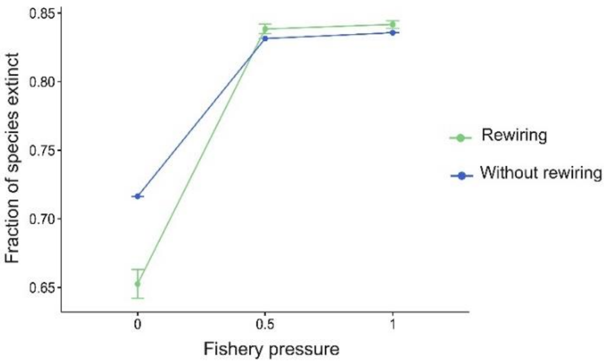

Fig. 1. Fraction of species extinct on the coastal marine food web in the tropical Pacific region as a function of fishery pressure in a scenario with rewiring (green line) and without rewiring (blue line) of interactions (filled dot = mean, error bars = SD). Results are based on 100 replicate food webs on each scenario.

In terms of trophic levels, the primary producers (TL1) and species of trophic level 4 were less prone to extinctions in both scenarios, compared with the other trophic levels (Fig. 2, Table S1). Among the species of trophic level 4 dying out in the model, there are several invertebrate species, such as *Portunus asper* and *Squilla panamensis* and elasmobranch species as the Leopard numbfish *Narcine leoparda* and the Whitesnout guitarfish *Pseudobatos leucorhynchus* (Table S1).

Extinctions were higher in the scenarios with rewiring and in the medium and high fishery pressure, mainly for species of the intermediate (TL2, TL 3) and high trophic levels (TL5) (Fig. 2, Table 1). Among the extinct species of the trophic level 2, are shrimp species as *Metapenaeopsis beebei* and *Penaeus californiensis*. Among the extinct species of the trophic level 3 are *Squilla* and *Rimapenaeus* species, and for the trophic level 5 are shark species as the Scalloped hammerhead *Sphyrna lewini*, the Bull shark *Carcharhinus leucas,* and bony fishes as *Lutjanus* species (Table 1).

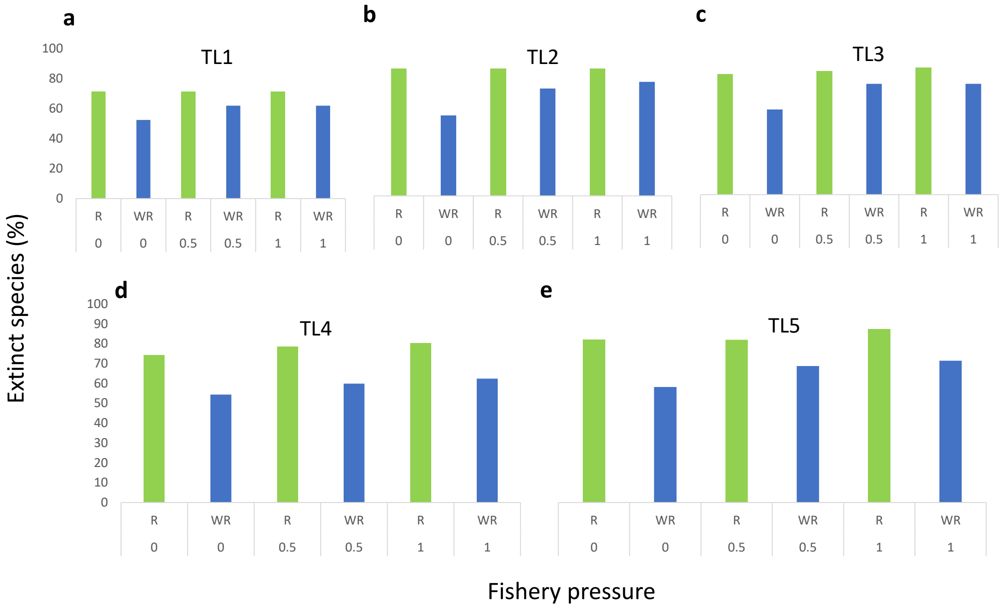

Fig. 2. Percentage of extinctions of species by trophic level (TL) in a coastal marine food web in the tropical Pacific region in function of Fishery pressure and under rewiring (R) and without rewiring events (WR), in the a) trophic level 1; b) trophic level 2; c) trophic level 3; d) trophic level 4 and e) trophic level 5. Results are based on 100 replicate food webs on each scenario.

In general, for the food web with rewiring, the mean abundances of species of all trophic level were higher in the low fishery pressure than in the scenario without rewiring and decreased in the intermediate and high fishery strength. In contrast, for the scenario without rewiring, the mean abundances increase in the intermediate fishery pressure for most trophic levels, except for primary consumers (TL2) (Fig. 3b) but showing similar main values of abundances in the food web with rewiring in the medium and high fishery pressure. The primary producers (TL1) was the group with higher abundances than the other trophic levels, even if they have slightly decreased under fishery strength (Fig. 3a), for both food web with and without rewiring; followed by species of intermediate (TL 4, TL2, TL3; Fig3d, b, c) and high trophic level (TL5) (Fig 3e).

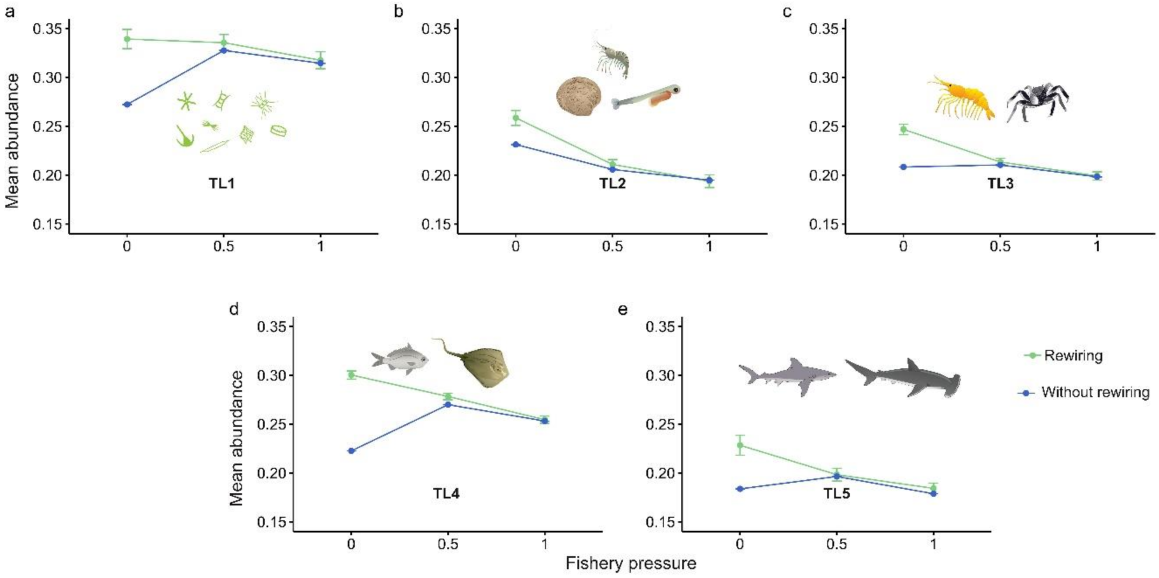

Fig. 3. Main abundance of species by trophic level (TL): a) trophic level 1, b) trophic level 2, c) trophic level 3, d) trophic level 4 and, e) trophic level 5, as function of fishery pressure, in a scenario with (green line) and without rewiring (blue line) of interactions (filled dot = mean, error bars = SD). Results are based on 100 replicate food webs on each scenario. Species symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

On the other hand, the resilience of the food web under rewiring of interactions was sharply lower and does not show major changes in relationship to the fishery pressure (Fig. 4). Additionally, the resilience of the food web under rewiring was lower than food web without rewiring in the low fishery pressure, but slightly higher for the intermediate and high level. In contrast, the resilience for the food web without rewiring decreased sharply in the intermediate fishery strength, and do not change in the high fishery pressure (Fig. 4).

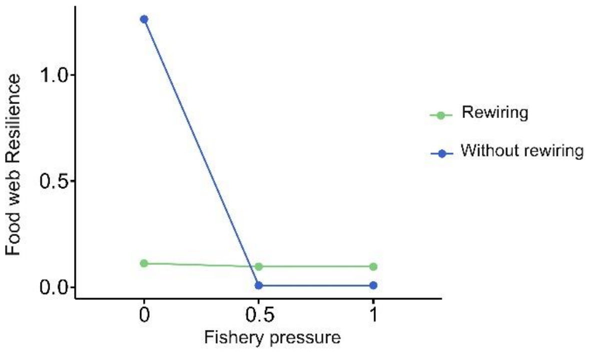

Fig. 4. Resilience of the coastal marine food web in the tropical Pacific region as a function of fishery pressure in a scenario with (green line) and without rewiring (blue line) of interactions (filled dot = mean, error bars = SD). Results are based on 100 replicate food webs on each scenario.

Considering this pattern, at medium and high fishery pressure, the mean abundances in the two scenarios with and without rewiring reached similar values, suggesting that rewiring has little effect under fishery pressure. These results indicate that the rewiring of interactions and the strength combinations here reported reduce the abundance of species, and with important implications for food web dynamics.

Discussion

The effect of changes of ecological interaction following anthropogenic events on community-level properties is key to understanding the dynamic responses of marine biodiversity (Ushio et al., 2018), aiming its maintenance and of their ecosystem services. We show that interaction rewiring under different fishing pressures strongly affect the abundances and extinctions of species through trophic levels, mainly species of higher trophic levels, as the generalist top predators, some of which are central species highly connected and with a wide effect within the network (see Marquez-Velásquez et al., 2021).

Considering that this coastal marine food web is highly connected (Marquez-Velásquez et al., 2021), the sharp decline of abundances of species across the whole food web, could be the result of chains of extinctions, facilitating in the long-term possible regime shifts and collapses of the food web. Indeed, evidence suggest that in this marine ecosystem the high-level predators are being replaced by intermediate trophic level species (Navia et al., 2010, 2016; Navia and Mejía-Falla, 2016). Another possible cause of the observed effects on abundances, with possible bottom-up and top-down processes involved, could be due to the increase of predation pressure on the remaining prey species by the rewiring of interactions following loss of prey species (Newsome et al., 2010; Gilljam et al., 2015; Prop et al., 2015), and with additional pressure of the multi-species and non-selective fisheries in the region.

Since human harvesters are examples of efficient consumers (Pauly et al., 1998; Brashares et al., 2004; Smith et al., 2011; Bonhommeau et al., 2013) and their effects top-down can be strong, the new resource species may die out, a point at which the interactions and their cascading effects change again (Wollrab et al., 2012; Sanders et al., 2013; Gilljam et al., 2015). Additionally, and in contrast to its adaptive feature of fisheries (Bertrand et al., 2007; Sethi et al., 2010), the multi-species fishery in this region does not rewire their interactions via adaptive target shifts, thus, it suggests a strong and constant pressure on remaining prey and predators after each rewiring event, that not only driving the primary and secondary extinctions, but also increases the vulnerability in terms of resilience of the food web following the rewiring of interactions.

In most of our scenarios several top predators are lost, such as the central and connected species of *Sphyrna* sharks, which may be one of the drivers of the response of the food web in terms of abundance and resilience. However, some models have shown that although food webs are least robust to the loss of generalist species (Eklof and Ebenman 2006; Curtsdotter et al., 2011), even the loss of interactions involving specialist species can also lead to the extinction of indirectly linked species from the same levels (Sanders et al., 2013), as the several main prey species as shrimps and bony fishes that were projected extinct in this study. As reported for some marine networks, the sharp decline in abundance of large marine coastal fish caused by intense human exploitation leading to different direct and indirect prey switching, which finally can lead to local collapse on the ecosystems (Estes et al., 1998; Springer et al., 2003; Brashares et al., 2004), which may be happening with our system. It is important to consider for future research how the dispersal of large size species among local communities might influence the impact of rewiring, since spatial processes has been suggested to have a destabilizing as well as a stabilising effect on ecological networks (Holyoak et al., 2005; McCann et al., 2005).

Since resilience is the measure of the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behavior (Walker et al., 1969, Holling 1996), is possible that the multiple extinctions that were generated, at different trophic levels, strongly affected this community properties. Additionally, the food web showed negative effects of rewiring affecting fluctuations of abundances, such as those generated by fisheries (but see Kondoh et al., 2003). Resilience and some community properties have been linked to diversity (Kondoh et al., 2003), and considering in our model the high number of extinctions of species (>30%) it may be more difficult for the system to bear the disturbances without having strong structural and dynamic responses (Springer et al., 2003; Brashares et al., 2004), as several species that are lost play different functional roles.

This first step in the exploration about the dynamic of this anthropogenic marine food web indicate that rewiring and the fishery pressure may potentially aggravate the consequences of the loss of species, possibly triggering extinction cascades, affecting the resilience and causing strong changes in the structure and dynamics of the coastal marine ecosystems. The next research step is to include and explore in the model empirical data of fishery strength, the ontogenetic changes of diet of species and the combination of parameters of life history of species that will permit a more accurate modelling, and thus promote strategies of management aiming the persistence of marine biodiversity and the ecosystem services in this coastal region in the tropical Pacific Ocean.

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Supplemental material

TABLE S1. Number of times that species are extinct by trophic level (TL), within the 100 replicates, on each scenario of fishery strength (FS) and with and without rewiring.

		Rewiring			**Without Rewiring**		
Trophic component	**TL**	**SF 0**	**SF 0.5**	**SF 1**	**SF 0**	**SF 0.5**	**SF 1**
Acantholithium	1	0	0	0	0	0	0
Acanthometra	1	0	0	0	0	0	0
Algae	1	0	0	0	0	0	0
Biddulphia	1	100	100	100	0	0	0
Ceratium	1	100	100	100	0	0	0
Chaetoceros	1	100	100	100	0	0	0
Cyanobacterias	1	62	100	100	0	0	0
Coscinodiscus	1	0	0	0	0	0	0
Detritus	1	100	100	100	0	0	0
Diatoms	1	100	100	100	0	0	0
Dinoflagellates	1	1	6	4	0	0	0
Ditylum	1	0	0	0	0	0	0
Phytoplankton	1	24	34	51	0	0	0
Macroalgae	1	0	0	0	0	0	0
Melosira	1	100	100	100	0	0	0
Navicula	1	88	100	100	0	0	0
Peridinium	1	100	100	100	0	0	0
Rhizosolenia	1	100	100	100	0	0	0
Skeletonema	1	100	100	100	0	0	0
Sphaerozoum	1	100	100	100	0	0	0
Triposolenia	1	29	100	100	0	0	0
Acanthochiasma	2	0	0	0	0	0	0
Holacanthida	2	0	0	0	0	0	0
Alpheus sp.	2	0	0	0	100	100	100
Anomura	2	0	0	0	0	0	0
Astrolithidae	2	0	0	0	100	100	100
Bivalves	2	100	100	100	100	100	100
Shrimps	2	87	100	100	0	0	0
Carditidae	2	85	100	100	0	0	0
Cetengraulis mysticetus	2	4	7	36	0	0	0
Chaetognats	2	44	48	61	0	0	0
Chloroscombrus sp.	2	95	100	100	0	0	0
Cavoliniidae	2	0	0	0	0	0	0
Echinoderms	2	5	6	41	0	0	0
Euphausiacea	2	100	100	100	0	0	0
Gigartaconidae	2	1	4	5	100	100	100

Ichthyoplankton	2	100	100	100	0	0	0
Metapenaeopsis beebei	2	100	100	100	100	100	100
Mugil curema	2	100	100	100	100	100	100
Nemertea	2	95	28	100	100	100	100
Nucula	2	100	100	100	100	100	100
Oligochaeta	2	100	100	100	0	0	0
Olividae	2	0	0	0	0	0	0
Pasiphaeidae	2	90	100	100	0	0	0
Penaeidae	2	100	100	100	0	0	0
Penaeus californiensis	2	100	100	100	100	100	100
Penaeus occidentalis	2	94	100	100	0	0	0
Penaeus spp.	2	100	100	100	100	100	100
Litopenaeus stylirostris	2	73	100	100	100	100	100
Litopenaeus vannamei	2	81	100	100	100	100	100
Polyplacophora	2	89	100	100	0	100	100
Polystira	2	94	100	100	100	100	100
Processa peruviana	2	49	100	100	100	100	100
Processa sp.	2	71	100	100	100	100	100
Processidae	2	90	100	100	0	0	0
Pteropoda	2	100	100	100	0	100	100
Scyphozoa	2	100	100	100	100	100	100
Sicyonia picta	2	83	100	100	100	100	100
Solenocera agassizii	2	68	100	100	100	100	100
Solenocera sp.	2	67	100	100	100	100	100
Tellinidae	2	53	100	100	100	0	100
Plagiacantha	2	91	100	100	100	100	100
Collodaria	2	85	100	100	100	100	100
Turtles	2	68	100	100	0	0	0
Triplasia	2	16	100	100	100	0	0
Zooplankton	2	38	100	100	100	100	100
Alpheidae	3	0	0	0	0	0	0
Aluterus sp.	3	0	0	0	0	100	100
Ambidexter panamensis	3	0	0	0	0	100	100
Anchovia macrolepidota	3	0	0	0	100	100	100
Ascidians	3	100	100	100	0	100	100
Brachyura	3	0	0	0	100	100	100
Brotula clarkae	3	0	0	0	0	0	0
Cancer johngarthi	3	94	100	100	100	100	100
Crabs	3	100	100	100	0	100	100
Capitellidae	3	93	100	100	100	100	100
Chloroscombrus orqueta	3	94	100	100	0	0	0
Cirratulidae	3	90	100	100	100	100	100
Cirripedians	3	40	58	50	0	0	0
Cladocerans	3	87	100	100	0	0	0

Copepods	3	8	3	44	0	0	0
Corallanidae	3	0	0	0	0	0	0
Crustaceans	3	0	0	0	0	0	0
Cumacea	3	0	0	0	0	0	0
Cymatidae	3	22	47	62	0	0	0
Dorippidae	3	100	100	100	0	0	0
Drilonereis	3	0	0	0	0	0	0
Ethusa ciliatifrons	3	55	51	52	0	0	0
Eunice sp.	3	0	0	0	0	0	0
Eunicidae	3	96	100	100	0	0	0
Euphylax robustus	3	88	100	100	0	0	0
Eurypanopeus transversus	3	100	100	100	0	0	0
Gammaridea	3	0	0	0	100	100	100
Glycera	3	0	0	0	100	100	100
Glyceridae	3	0	0	1	100	100	100
Goneplacidae	3	100	100	100	100	100	100
Goniada	3	100	100	100	0	0	0
Goniadidae	3	52	60	51	100	100	100
Goniadides sp.	3	0	0	0	0	0	0
Goniopsis pulchra	3	0	0	0	0	0	0
Grapsidae	3	100	100	100	100	100	100
Grapsus grapsus	3	0	5	33	100	100	100
Hepatus kossmanni	3	100	100	100	0	0	0
Hepatus sp.	3	100	100	100	100	100	100
Persephona subovata	3	91	100	100	0	0	0
Inachoididae	3	89	100	100	0	0	0
Leucosiidae	3	100	100	100	0	0	0
Luciferidae	3	100	100	100	100	100	100
Lumbrineridae	3	0	2	7	0	0	0
Majidae	3	100	100	100	0	0	0
Mugilidae	3	100	100	100	100	0	100
Mysida	3	57	54	38	100	0	100
Nephtyidae	3	100	100	100	0	0	0
Nereididae	3	100	100	100	100	100	100
Nereis	3	0	0	1	100	100	100
Ocypode spp.	3	100	100	100	100	100	100
Oenonidae	3	100	100	100	100	0	0
Onuphidae	3	100	100	100	100	100	100
Opisthonema libertate	3	100	100	100	0	0	0
Opisthonema spp.	3	100	100	100	100	100	100
Ostracoda	3	100	100	100	0	0	0
Pachygrapsus transversus	3	100	100	100	100	100	100
Palaemon sp.	3	100	100	100	100	100	100
Pandalidae	3	52	100	100	0	0	0

Panopeus purpureus	3	90	100	100	0	0	0
Paradasygyius depressus	3	100	100	100	0	0	0
Parthenope sp.	3	89	100	100	0	0	0
Pectinariidae	3	83	100	100	0	0	0
Penaeus brevirostris	3	90	100	100	0	0	0
Phyllodocidae	3	91	100	100	0	0	0
Phyllostauros	3	84	100	100	100	100	100
Pinnotheridae	3	88	100	100	100	100	100
Polychaeta	3	93	100	100	0	0	0
Portunidae	3	79	100	100	0	0	0
Protrachypene precipua	3	83	100	100	0	0	0
Pycnogonidae	3	76	100	100	0	0	0
Raninoides benedicti	3	100	100	100	0	0	0
Ranellidae	3	100	100	100	100	100	100
Rimapenaeus byrdi	3	100	100	100	0	0	0
Rimapenaeus faoe	3	100	100	100	100	0	100
Rimapenaeus fuscina	3	38	100	100	0	0	0
Rimapenaeus pacificus	3	100	100	100	0	0	0
Rimapenaeus spp.	3	90	100	100	0	0	0
Sergia inoa	3	100	100	100	0	0	0
Sesarma rhizophorae	3	100	100	100	0	0	0
Sipuncula	3	83	100	100	0	0	0
Solenoceridae	3	58	100	100	0	0	0
Spionidae	3	81	100	100	100	100	100
Squilla aculeata	3	100	100	100	100	100	100
Squilla biformis	3	74	100	100	100	0	0
Squilla mantoidea	3	100	100	100	0	0	0
Stenocionops ovatus	3	80	100	100	100	100	100
Stenorhynchus debilis	3	79	100	100	0	0	0
Sternaspidae	3	86	100	100	0	0	0
Terebellidae	3	13	100	100	100	100	100
Trachypenaeus pacificus	3	100	100	100	0	100	100
Trachypenaeus spp.	3	100	100	100	0	100	100
Ucides occidentalis	3	37	100	100	100	100	100
Xiphopenaeus kroyeri	3	36	100	100	0	100	100
Xiphopenaeus sp.	3	55	100	100	0	100	100
Abraliopsis spp.	4	0	0	0	0	0	0
*Achirus klunzingeri**	4	0	0	0	0	0	0
Achirus mazatlanus	4	0	0	0	0	0	0
Albuneidae	4	0	0	0	100	100	100
Amphipoda	4	0	0	0	100	100	100
Anchoa spp.	4	0	0	0	100	100	100
Anchoa starksi	4	0	0	0	100	100	100
Anguilliformes	4	0	0	0	0	0	0

Anisotremus sp.	4	0	0	0	0	0	0
Aratus pisonii	4	0	0	0	0	0	0
Arenaeus mexicanus	4	100	100	100	100	100	100
Ariidae	4	0	0	0	100	100	100
Ariopsis seemanni	4	100	100	100	0	0	0
Aulopiformes	4	0	0	0	0	0	0
Axiidae	4	0	0	0	100	100	100
Bagre panamensis	4	0	0	0	100	100	100
Balistidae	4	0	0	0	100	100	100
Bathygobius sp.	4	0	0	0	100	100	100
Batoidea	4	0	0	1	100	100	100
Batrachoididae	4	1	7	41	0	0	0
Benthesicymus tanneri	4	0	0	0	0	0	0
Bollmannia chlamydes	4	100	100	100	100	100	100
Bothidae	4	100	100	100	100	100	100
Bregmaceros bathymaster	4	0	0	0	100	100	100
Bucciniade	4	0	0	0	100	100	100
Calappidae	4	72	100	100	100	100	100
Callinectes arcuatus	4	1	7	32	100	100	100
Callinectes spp.	4	96	100	100	100	100	100
Callinectes toxotes	4	100	100	100	100	100	100
Caridea	4	100	100	100	100	100	100
Cephalopods	4	97	30	100	100	100	100
Centropomus unionensis	4	92	100	100	100	100	100
Chaenopsidae	4	78	49	35	100	100	100
Chromis spp.	4	93	100	100	0	0	0
Citharichthys gilberti	4	100	100	100	0	0	0
Cloridopsis dubia	4	100	100	100	100	0	0
Clupeidae	4	2	4	35	100	0	0
Clupeiformes	4	88	100	100	100	100	100
Cnidarians	4	0	0	0	100	100	100
Congridae	4	27	53	51	100	100	100
Cyclopsetta querna	4	0	0	0	100	0	100
Cynoglossidae	4	0	0	0	100	100	100
Cynoscion phoxocephalus	4	1	39	48	100	100	100
Dendrobranchiata	4	100	100	100	100	100	100
Diapterus sp.	4	100	100	100	100	100	100
Diogenidae	4	100	100	100	0	0	0
Diplectrum	4	0	2	4	0	0	0
Echiophis brunneus	4	100	100	100	100	100	100
Emerita sp.	4	0	0	0	100	100	100
Engraulidae	4	0	0	1	100	100	100
Stomatopods	4	100	100	100	0	0	0
Eucinostomus spp.	4	0	2	4	0	0	0

Eugerres lineatus	4	94	34	100	100	100	100
Eugerres brevimanus	4	92	29	100	100	100	100
Euphylax sp.	4	84	45	12	100	100	100
Exocoetidae	4	53	47	51	0	0	0
Galappidae	4	97	100	100	0	0	0
Galatheidae	4	91	100	100	100	100	100
Gastropoda	4	0	0	0	100	100	100
Gobiidae	4	0	0	1	100	100	100
Gonatus onyx	4	0	0	0	100	100	100
Gonodactylidae	4	3	4	36	100	100	100
Gonostomatidae	4	0	1	6	100	100	100
Guyanacaris caespitosa	4	99	25	100	100	100	100
Gymnotorax equatorialis	4	0	2	5	100	0	0
Harengula thrissina	4	0	0	0	100	100	100
Haemulopsis nitidus	4	0	4	4	100	100	100
Halichoeres aestuaricola	4	0	0	0	100	100	100
Halichoeres chierchiae	4	0	0	0	100	100	100
Halichoeres dispilus	4	47	55	47	100	100	100
Halichoeres notospilus	4	37	56	57	100	100	100
Hippidae	4	63	44	36	0	100	100
Hyaloteuthis pelagica	4	100	100	100	0	100	100
Hypanus longus	4	23	55	55	100	100	100
Ichthyapus selachops	4	0	2	9	100	100	100
Isopoda	4	100	100	100	100	100	100
Larimus argenteus	4	92	100	100	100	100	100
Larimus spp.	4	0	0	0	0	100	100
Leachia danae	4	0	0	0	100	100	100
Flatfishes	4	0	0	0	100	100	100
Lile stolifera	4	100	100	100	100	100	100
Loliginidae	4	100	100	100	100	100	100
Doryteuthis (Amerigo) *gahi*	4	100	100	100	100	100	100
Loligo sp.	4	49	55	50	100	100	100
Lolliguncula argus	4	47	47	64	100	100	100
Lolliguncula diomedae	4	50	58	57	100	100	100
Lolliguncula panamensis	4	100	100	100	100	100	100
Lysiosquilla sp.	4	92	100	100	100	100	100
Lysiosquillidae	4	100	100	100	100	100	100
Lysiosquilla panamica	4	100	100	100	0	100	100
Macrobrachium americanum	4	4	3	32	0	100	100
Meiosquilla dawsoni	4	100	100	100	100	100	100
Michalisquilla parva	4	100	100	100	100	100	100
Mollusca	4	100	100	100	0	100	100
Munida	4	100	100	100	100	100	100
Munida obesa	4	100	100	100	100	100	100

Muraena sp.	4	100	100	100	100	100	100
Mustelus lunulatus	4	0	0	0	100	100	100
Narcine leoparda	4	100	100	100	0	0	100
Decapoda	4	100	100	100	100	100	100
Neodoclea boneti	4	100	100	100	0	100	100
Neogonodactylus stanschi	4	100	100	100	100	100	100
Ogyrides alphaerostris	4	35	61	64	100	100	100
Ogyrididae	4	47	55	65	100	100	100
Onychoteuthis banksii	4	100	100	100	0	100	100
Ophichthidae	4	100	100	100	100	100	100
Ophichthus frontalis	4	100	100	100	0	100	100
Ophioscion strabo	4	100	100	100	100	100	100
Opisthopterus sp.	4	50	54	46	100	100	100
Palicidae	4	100	100	100	100	100	100
Palaemonidae	4	100	100	100	0	100	100
Pleocyemata	4	100	100	100	100	100	100
Paralonchurus petersii	4	9	100	100	0	100	100
Parasquilla similis	4	93	100	100	0	100	100
Perciformes	4	87	100	100	100	100	100
Petrolisthes zacae	4	93	100	100	100	100	100
Pleuronectiformes	4	79	100	100	100	100	100
Polydactylus approximans	4	100	100	100	100	100	100
Polydactylus opercularis	4	100	100	100	100	100	100
Polynemidae	4	100	100	100	0	100	100
Pomadasys panamensis	4	93	100	100	100	100	100
Porcellanidae	4	100	100	100	100	100	100
Porichthys spp.	4	100	100	100	100	100	100
Porichthys margaritatus	4	67	100	100	100	100	100
Portunus asper	4	100	100	100	100	100	100
Portunus spp.	4	77	100	100	100	100	100
Portunus xantusii	4	100	100	100	100	100	100
Prionotus horrens	4	100	100	100	0	100	100
Pristigasteridae	4	52	100	100	100	100	100
Pseudobatos leucorhynchus	4	100	100	100	100	100	100
Pseudupeneus grandisquamis	4	81	100	100	0	100	100
Pseudosquillidae	4	100	100	100	100	100	100
Raja velezi	4	76	100	100	100	100	100
Sciaenidae	4	100	100	100	100	100	100
Scorpaeniformes	4	100	100	100	100	100	100
Selene peruviana	4	78	100	100	100	100	100
Sphoeroides annulatus	4	100	100	100	100	100	100
Sphyrna tiburo	4	86	100	100	0	100	100
Squilla panamensis	4	100	100	100	100	100	100
Squilla sp.	4	75	100	100	100	100	100

Squillidae	4	85	100	100	0	100	100
Stellifer fuerthii	4	100	100	100	0	100	100
Stellifer melanocheir	4	84	100	100	100	100	100
Stellifer oscitans	4	84	100	100	100	100	100
Stellifer sp.	4	100	100	100	0	100	100
Stellifer zestocarus	4	75	100	100	100	100	100
Sicyonia disdorsalis	4	100	100	100	100	100	100
Sicyonia sp.	4	90	100	100	100	100	100
Sicyoniidae	4	100	100	100	0	100	100
Symphurus elongatus	4	100	100	100	0	100	100
Symphurus sp.	4	100	100	100	100	100	100
Terebridae	4	15	100	100	100	100	100
Decapodiformes	4	47	100	100	100	100	100
Thalassinidea	4	60	100	100	100	100	100
Thalassoma lucasanum	4	83	100	100	100	100	100
Trinectes fonsecensis	4	9	100	100	0	100	100
Urotrygon aspidura	4	8	100	100	100	100	100
Urotrygon rogersi	4	47	100	100	100	100	100
Urotrygon spp.	4	100	100	100	100	100	100
Xanthidae	4	26	100	100	0	100	100
Xiphopenaeus riveti	4	0	100	100	100	100	100
Zapteryx xyster	4	33	100	100	100	100	100
Aetobatus narinari	5	0	0	0	100	100	100
Anchoa spinifer	5	0	0	0	100	100	100
Beloniformes	5	100	100	100	0	100	100
Carangidae	5	100	100	100	0	0	100
Caranx caninus	5	71	40	36	100	100	100
Caranx sp.	5	95	100	100	100	100	100
Carcharhinus leucas	5	100	100	100	0	100	100
Cathorops manglarensis	5	94	100	100	100	100	100
Cynoscion sp.	5	0	0	0	100	100	100
Cynoscion analis	5	0	0	0	100	100	100
Dosidicus gigas	5	100	100	100	100	100	100
Fistularia sp.	5	100	100	100	100	100	100
Histioteuthis cf. *heteropsis*	5	44	52	58	100	100	100
Katsuwonus pelamis	5	95	100	100	0	100	100
Lutjanus argentiventris	5	0	0	2	0	100	100
Lutjanus guttatus	5	100	100	100	100	100	100
Lutjanus peru	5	100	100	100	100	100	100
Macrodon mordax	5	100	100	100	0	100	100
Mustelus henlei	5	0	0	0	0	100	100
Myrophis vafer	5	53	56	43	100	100	100
Notarius troschelii	5	0	0	2	0	100	100
Oligoplites sp.	5	100	100	100	100	100	100

Oligoplites refulgens	5	100	100	100	100	100	100
Ommastrephes bartramii	5	49	61	55	100	100	100
Paralichthyidae	5	93	100	100	100	100	100
Scomberomorus sierra	5	70	100	100	0	100	100
Scombridae	5	100	100	100	100	100	100
Sphyraena sp.	5	84	100	100	0	100	100
Sphyraenidae	5	83	100	100	0	100	100
Sphyrna corona	5	82	100	100	0	100	100
Sphyrna lewini	5	100	100	100	0	100	100
Sphyrna media	5	63	100	100	100	100	100
Sthenoteuthis oualaniensis	5	92	100	100	0	100	100
Strongylura sp.	5	87	100	100	0	100	100
Synodontidae	5	100	100	100	100	100	100
Thunnus albacares	5	84	100	100	0	100	100
Trichiurus lepturus	5	34	100	100	0	100	100
Trichuridae	5	100	100	100	0	100	100

CONSIDERAÇÕES FINAIS

A abordagem da teoria de redes, junto com a teoria ecológica e com dados empíricos de interações tróficas de ecossistemas marinhos costeiros, permite cada vez mais uma melhor compreensão da complexidade destes sistemas e das suas respostas aos impactos antropogênicos os quais geram profundas mudanças em termos de biodiversidade e funções ecossistêmicas. Ademais permitem explorar quais são os fatores intrínsecos que potencialmente influenciam a sua manutenção, um desafio crítico para este século.

Existem evidências teóricas de *drivers* da estrutura e dinâmica das redes tróficas marinhas, que representam potenciais aspectos a serem avaliados em campo e colocados em prática em estratégias de gestão e manejo, visando a manutenção dos serviços ecossistêmicos que sustentam diretamente as comunidades costeiras em termos econômicos e de segurança alimentar, principalmente em países em desenvolvimento na região tropical.

Os nossos resultados contribuem para a emergente abordagem socio-ecológica no estudo de redes, resultado da modelagem da estrutura e dinâmica de uma rede trófica marinha. Para a rede trófica do Pacífico centro sul colombiano, além de ter evidenciado a importância de espécies de tubarões martelo -*Sphyrna*- na estrutura e dinâmica da rede trófica, identificamos o papel central da pesca artesanal, principalmente a pesca não seletiva de arrastro de camarão, agindo como um dos principais motores da dinâmica ecológica e possivelmente evolutiva do sistema. É importante considerar que a pesca e as espécies de predadores de topo e mesopredadores exibem interações diretas complementares, mas efeitos indiretos altamente sobrepostos, os quais podem potencializar os efeitos através da rede. Neste ponto fica aberta a questão sobre a dinâmica dos efeitos secundários induzidos pela pesca em sistemas tropicais altamente diversos e com um contexto socioambiental complexo. A avaliação dos efeitos secundários nos modelos dinâmicos das redes tróficas representa um avanço significativo na compreensão de como a reconfiguração das interações e as extinções secundárias de espécies podem influenciar a resiliência e estabilidade dos ecossistemas marinhos.

Em relação a dinâmica ecológica abordada, é preciso explorar e ajustar o modelo aos diferentes parâmetros biológicos e ecológicos. A modelagem dinâmica com uso de dados empíricos representa um grande desafio para a pesquisa ecológica que pode e deve ser aplicada e integrada a traves das diferentes escalas espaciais e temporais, para capturar a dinâmica das espécies com diferentes histórias de vida e que podem apresentar mudanças ontogenéticas nas suas dietas. A validação dos modelos dinâmicos com dados empíricos, permitirá ao longo prazo tomar decisões mais apropriadas sobre conservação e gestão das espécies.

Considerando a complexidade social e econômica ligada a atividade da pesca nas regiões tropicais, e particularmente na área de estudo (Rueda et al., 2011; Saavedra- Díaz et al., 2015), é importante não apenas explorar as dinâmicas ecológicas e evolutivas das espécies, mas também incluir as dinâmicas sociais e económicas, e como elas são reconfiguradas em relação às reconfigurações das interações das espécies. Assim, para estes sistemas socioecológicos, a aplicação da abordagem de redes multicamadas (Kivelä et al., 2014; Bodim et al., 2019; Sayles et al., 2019; Jacob et al., 2020) é sugerida com uma opção pertinente para futuras pesquisas, que permite abordar os complexos desafios da gestão de recursos e da governança, incorporando interações entre e através dos sistemas sociais, económicos e ecológicos (Kivelä et al., 2014; Pilosof et al., 2017; Bodin et al., 2019; Sayles et al., 2019; Kluger et al., 2020). Sintetizar a abordagens ecológica e socioeconômica pode melhorar as bases críticas de evidências, para onde as ações de conservação devem ser direcionadas e testadas (Sutherland et al., 2018).

Nossos resultados são dados preliminares e um ponto de partida para subsidiar pesquisas inovadoras em regiões costeiras de países em desenvolvimento, combinando os modelos dinâmicos de redes e o monitoramento ao longo prazo, que visem a conservação e manutenção da biodiversidade marinha e os serviços ecossistêmicos como a pesca. Os dados de campo resultantes de monitoramento permitiram avaliar as previsões e pressupostos dos modelos subjacentes às estratégias de conservação propostas. Entre os componentes das futuras pesquisas, é sugerido elaborar medidas experimentais para reduzir as capturas incidentais, por exemplo explorando outras artes de pesca; e a recuperação demográfica de populações das espécies ameaçadas e identificadas como as mais centrais na rede trófica.

Finalmente, este tipo de pesquisa deixa evidente a necessidade de uma abordagem interdisciplinar no estudo da dinâmica das redes tróficas dos ecossistemas marinhos, articulando diversos campos de pesquisa ecológica, biológica e de modelagem, baseados no componente teórico e experimental. Ademais é relevante para as medidas de conservação propostas a partir dos resultados deste tipo de abordagem, envolver aos diferentes agentes sociais, como os pescadores artesanais, que facilitem a implementação deste tipo de medidas e assim lograr um trabalho articulado e interdisciplinar entre academia, comunidades locais e órgãos de tomada de decisões, com o objetivo de preservar os serviços ecossistêmicos como a segurança alimentar e o bem estar das comunidades locais que dependem da pesca.

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