UNIVERSIDADE FEDERAL DE ALAGOAS

INSTITUTO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos

LARISSA DE JESUS BENEVIDES

O COMPORTAMENTO E A ANTECIPAÇÃO DO RISCO EM PEIXES TERRITORIAIS SOB INFLUÊNCIA DO MERGULHADOR

Maceió – Alagoas
Fevereiro/ 2020

LARISSA DE JESUS BENEVIDES

O COMPORTAMENTO E A ANTECIPAÇÃO DO RISCO EM PEIXES TERRITORIAIS SOB INFLUÊNCIA DO MERGULHADOR

Tese apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, como requisito para obtenção do título de Doutora em CIÊNCIAS BIOLÓGICAS, área de concentração em Biodiversidade.

Orientador: Dr. Cláudio L. S. Sampaio

Co-orientadores: Dr. Pedro H. C. Pereira e Dra. Taciana P. Kramer

Maceió – Alagoas
Fevereiro/ 2020

Catalogação na fonte
Universidade Federal de Alagoas
Biblioteca Central
Divisão de Tratamento Técnico
Bibliotecário: Marcelino de Carvalho Freitas Neto – CRB-4 - 1767

B465c Benevides, Larissa de Jesus.
O comportamento e a antecipação do risco em peixes territoriais sob influência do mergulhador / Larissa de Jesus Benevides. – 2020.
138 f. : il.

Orientador: Cláudio L. S. Sampaio.
Co-orientador: Pedro H. C. Pereira.
Co-orientadora: Taciana P. Kramer.
Tese (Doutorado em Ciências Biológicas) – Universidade Federal de Alagoas. Instituto de Ciências Biológicas e da Saúde. Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos. Maceió, 2020.

Inclui bibliografias.

1. Distúrbio-do-mergulhador. 2. *Pomacentridae*. 3. Forrageamento. I. Título.

CDU: 616-008.64

UNIVERSIDADE FEDERAL DE ALAGOAS

Instituto de Ciências Biológicas e da Saúde

PPG-DIBICT

Ata da banca de defesa da Tese do Programa de Pós-Graduação em Diversidade Biológica e Conservação (PPG-DIBICT), de **Larissa de Jesus Benevides** realizada dia 28 de fevereiro de 2020.

Às treze horas e trinta minutos do vigésimo oitavo dia do mês de fevereiro de 2020, reuniu-se para a primeira (1ª) defesa pública de Tese do Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos do Instituto de Ciências Biológicas e da Saúde/ICBS da Universidade Federal de Alagoas/UFAL, no Instituto de Ciências Biológica e da Saúde da UFAL a banca composta pelos professores doutores avaliadores: Vinicius José Giglio/UFF, Jean Christophe Joyeux/UFES, Robson Guimarães dos Santos/UFAL, Vandick da Silva Batista/UFAL, Hudson Tercio Pinheiro/California Academy of Sciences e com a presença do Prof. Dr. Cláudio Luís Santos Sampaio/UFAL (orientador), para avaliar a tese da doutoranda Larissa de Jesus Benevides. Durante a apresentação foi avaliada a compatibilidade do trabalho de pesquisa com o nível de doutorado e a autoria da discente, sendo arguido a doutoranda foi capaz de responder pelas informações e procedimentos apresentados. Também foi avaliado se a tese contém produção científica para gerar dois artigos para revista científica com QUALIS A, conforme comitê de Biodiversidade da CAPES. Em formulários anexos a esta ata, constam os pareceres finais de cada membro da banca. A defesa pública foi APROVADA. Sendo o ato de defesa finalizado foi lavrada a presente ata que por todos será assinada.

Prof. Dr. Vinicius José Giglio/UFF
(membro titular)

Prof. Dr. Jean Christophe Joyeux/UFES
(membro titular)

Prof. Dr. Robson Guimarães dos Santos/UFAL
(membro titular)

Prof. Dr. Vandick da Silva Batista/UFAL
(membro titular)

Prof. Dr. Cláudio Luís Santos Sampaio/UFAL
(orientador)

Hudson Tercio Pinheiro/California Academy of Sciences
(membro titular)

Larissa de Jesus Benevides
(doutoranda)

AGRADECIMENTOS

Agradeço aos meus pais, Clícia e Jofre, por terem trabalhado e abdicado tempo de suas vidas para se dedicarem à minha educação (e do meu irmão). Sou privilegiada, apesar das dificuldades, de ter seguido meu objetivo de ser bióloga marinha e de estar concluindo este doutorado. Às minhas avós, Lourdes e Rosete, agradeço aos ensinamentos sobre cuidado, respeito, sabedoria para lidar com as adversidades da vida, e pelo troco do pão. Às tias, tios, primos, sogro, sogra, cunhada, cunhado, afilhada, Astro (o cachorro), aos amigos presentes e imaginários, obrigada pelo carinho e sorrisos compartilhados a cada reencontro.

Aos amigos Robson e Louisa, serei eternamente grata pelo abrigo, conversas, conselhos e apoio emocional ao longo da construção desta tese.

Especialmente, agradeço ao meu irmão, Leandro, por me encorajar e acreditar que eu sou muito mais do que acredito ser. Obrigada por compartilhar seus medos e alegrias. Por ouvir minhas aventuras acima e debaixo d'água, minhas histórias (verdadeiras ou não), minhas piadas, e por abrir os gifs que eu cuidadosamente escolho para lhe enviar. Obrigada por ter incansavelmente escutado minhas aflições acadêmicas durante o doutorado.

Finalmente, agradeço ao meu companheiro na vida e na ciência, Gabriel, por pacientemente ter se aventurado ao meu lado nesta saga em busca do título de Doutora, e por compartilhar horas de discussões sem fim sobre o comportamento dos peixes. Seu apoio desde a construção das ideias, trabalhos de campo, análise dos dados, até a escrita, foram fundamentais para que esta tese fosse moldada. Obrigada por sua cumplicidade, por me manter alimentada e por ter cuidado da minha sanidade (além de lembrar de pagar as contas, molhar as plantas, levar minha vó na feira, no mercado, no médico, levar Astro para o banho...).

Durante o doutorado, tive a honra de estar afiliada ao laboratório de Ictiologia – UFES e agradeço a todos pelo acolhimento e pelo intercâmbio de conhecimento científico e de vida. O suporte de vocês foi essencial.

Além da família e amigos, o desenvolvimento desta tese não teria sido possível sem o suporte dos coautores que participaram em cada capítulo, dos meus orientadores: Cláudio Sampaio, Pedro Pereira e Taciana Kramer, e do PPG-DIBICT. Sou muito grata a todos pelo apoio, incentivo, críticas e contribuições durante a construção deste trabalho.

“I tell you what freedom is to me: no fear. I mean, no fear.

If I could have that half of my life...”

Nina Simone (1933-2003)

SUMÁRIO

LISTA DE FIGURAS

II. FEAR-INDUCED BEHAVIOURAL MODIFICATIONS IN DAMSELFISHES CAN BE DIVER- TRIGGERED

III. THE DISRUPTIVE INFLUENCE OF HUMAN PRESENCE ON TERRITORIAL BEHAVIOUR OF TWO CORAL REEF DAMSELFISHES

IV. HUMAN INTIMIDATION ON REEFS IMPAIRS FORAGING RATES OF TERRITORIAL FISHES

Figure 1: Comparative display of *Stegastes sanctipauli* behaviour in absence of human or reef predator disturbance (A); in the presence of barracuda model (B); an occasional encounter between a reef predator, *Sphyraena barracuda,* and predator model (C); and in SCUBA diver presence (D). Red arrows highlight individuals under study.

Figure 2: Foraging rates of the damselfishes: *Stegastes sanctipauli* (A)*, Stegastes fuscus* (B)*, Pomacentrus wardi* (C) and *Stegastes apicalis* (D) under human disturbance treatment – HDT and control, in three distinct reef systems: remote island reef – SPSPA (A), recreational coastal reef - Arraial do Cabo, RJ – Brazil (B) and recreational mainland island reef - Magnetic island – Australia (C, D).

RESUMO

Animais moldam suas decisões de custo-benefício, associadas à alimentação e segurança, de acordo com a percepção do risco de predação. No ambiente marinho, mesmo atividades não-extrativistas, como o ecoturismo, podem elevar a cautela dos animais, induzindo-os a fugir ou procurar abrigo. Entretanto, os custos desta perturbação em animais associados ao habitat, permanecem subestimados. Isto inclui como eles balanceiam a defesa territorial e a ingestão de alimentos enquanto lidam com nossa presença no ambiente recifal. Entender esses efeitos é crucial para elucidar se o turismo de mergulho pode prejudicar a condição corporal dos peixes e/ou as interações interespecíficas. Nesta tese, investiguei se a presença de mergulhadores SCUBA e em mergulho livre, em sistemas recifais distintos, prejudica o comportamento de quatro espécies de peixes territoriais: *Stegastes fuscus, S. sanctipauli, S. apicalis e Pomacentrus wardi.* Abordagens experimentais (presença de mergulhadores, presença de modelo de predador, e controle) foram aplicadas em 125 territórios, usando câmeras de vídeo remotas subaquáticas. Os vídeos foram analisados no *Behavioral Observation Research Interactive Software (BORIS),* considerando a frequência dos comportamentos: refúgio, forrageamento, perseguição e tempo de patrulhamento. No geral, as respostas comportamentais indicam que a presença de mergulhadores reduz a frequência da defesa territorial e o tempo de patrulha, forçando os peixes a se refugiarem ao invés de se alimentarem. Adicionalmente, em um recife remoto, *S. sanctipauli* mostrou ampla generalização no reconhecimento de predadores, não distinguindo efetivamente os estímulos de ameaça entre o modelo de predador e presença do mergulhador. A presença humana transitória nos recifes intimida e reduz a exploração de alimentos por donzelinhas. Com essas mudanças, as relações tróficas entre peixes territoriais e a comunidade bentônica podem se tornar instáveis. Isto afetaria a resiliência das comunidades recifais tanto em áreas marinhas remotas e quanto recreativas. O monitoramento a longo-prazo do comportamento de peixes territoriais irá ampliar o conceito de paisagem do medo, além de servir como indicador de distúrbios humanos e, portanto, ser valioso para estratégias de conservação nos recifes de coral.

Palavras-chave: Distúrbio-do-mergulhador; Donzelinhas; Efeitos-não-letais; Forrageamento.

ABSTRACT

Animals shape their cost-benefit decisions, associated with food and safety, according to the perception of predation risk. In the marine environment, even non-consumptive human-related activities, such as ecotourism, can increase the animal's wariness, often inducing them to flee or seek shelter. Yet, the costs of this disturbance on site-attached animals, remain underestimated. It includes how they trade-off the territory defense and food intake while dealing with our ongoing presence in the reef systems. Understanding these effects is crucial to elucidating whether diving tourism can impair fish body condition and/or interspecific interactions. Here, I investigated if the presence of SCUBA divers and snorkelers, in distinct reef systems, can disrupt the behaviour of four damselfish species: *Stegastes fuscus*, *S. sanctipauli, S. apicalis* and *Pomacentrus wardi*. Experimental approaches (diver presence, predator decoy presence and control) were applied in 125 territories of damselfishes using underwater remote video cameras. All recorded videos were analysed in the Behavioral Observation Research Interactive Software (BORIS) by considering the frequency of following behaviours: refuge, foraging, chase and the patrolling time. Overall, behavioural responses indicate that diver presence reduced the frequency of territorial defence and patrolling time, pushing them to take refuge rather than feed. Additionally, at a remote reef, *S. sanctipauli* have shown a wide generalization of predator recognition, do not effectively distinguish the threat-stimuli between predator model and diver presence. The transient human presence in reefs intimidate and diminish damselfishes' food exploration. Withal these changes, the trophic relationships between territorial fish and benthic community may become unstable. It would affect the resilience of coral reef community in pristine and recreational marine areas. Long-term monitoring of the territorial fish behaviour will broaden the concept of landscape of fear, as well as work as an indicator of human disturbance and thus, be valuable for conservation strategies in coral reefs.

Keywords: Damselfishes; Diver-disturbance; Non-lethal effects; Foraging behaviour.

I. REVISÃO DE LITERATURA E APRESENTAÇÃO DA TESE

Por séculos, humanos têm transitado entre os ambientes terrestre e marinho, alterando suas paisagens em uma escala global. Por meio do comportamento predatório e contínua exploração dos recursos naturais, nos tornamos um 'super predador' (CLINCHY et al., 2016) e seguimos, insustentavelmente, afetando as relações ecológicas e processos evolutivos das espécies não-humanas (chamadas aqui como 'animais') (DARIMONT et al., 2015). Se você não é caçador ou pescador, talvez esteja pensando que não se enquadra na declaração acima. Pelo contrário. De modo geral, nós humanos representamos potencial ameaça para animais selvagens, mesmo não tendo a intenção de ferir ou matar (CIUTI et al., 2012; FRID; DILL, 2002). Assim como o efeito predatório, o distúrbio humano não-letal também é capaz de estabelecer uma 'paisagem do medo', elevando o investimento do indivíduo em comportamentos antipredatórios com o aumento da cautela (JANUCHOWSKI-HARTLEY et al., 2011; LAUNDRE; HERNANDEZ; RIPPLE, 2010; MADIN et al., 2016). Por isso, quando tentamos abordá-los, a primeira reação de muitos animais é fugir (BENEVIDES et al., 2018; BLUMSTEIN et al., 2003; NUNES et al., 2018; SAMIA et al., 2019).

Mesmo durante atividades recreativas podemos influenciar indireta e diretamente o comportamento das espécies. Por exemplo, ditando quando, onde, e de que os animais se alimentam. Isto pode afetar as taxas metabólicas do indivíduo e a estabilidade das relações interespecíficas dentro da estrutura de uma comunidade (BARNETT et al., 2016; BURGIN; HARDIMAN, 2015). No ambiente marinho, o mergulho recreativo é uma das principais atividades praticadas por turistas. O número de mergulhadores certificados (que utilizam aparelho de respiração subaquática autônomo - SCUBA) ou que praticam mergulho livre, cresce a cada ano (BARKER; ROBERTS, 2004; GIGLIO et al., 2017; HASLER; OTT, 2008). Embora ainda existam brechas no conhecimento acerca de seus impactos, pesquisas apontam que essas atividades prejudicam a sobrevivência de organismos marinhos (e.g. danos físicos), especialmente aqueles que vivem associados ao substrato, como os animais bentônicos sésseis (e.g. corais, crustáceos e esponjas) (DI FRANCO et al., 2009; GIGLIO; LUIZ; FERREIRA, 2020; ROCHE et al., 2016). Todavia, comunidades de

peixes recifais têm sido também negativamente afetadas pelo mergulho recreativo (GIGLIO et al., 2018; HAWKINS et al., 1999; TITUS; DALY; EXTON, 2015).

A redução na abundância de peixes herbívoros (que fogem com o aumento de turistas nos recifes), e consequentemente na herbivoria, sugere que a presença de mergulhadores pode modificar o efeito '*top-down*' (mediado pelo consumidor) no controle da cadeia trófica (GIL et al., 2015). Adicionalmente, a presença de mergulhadores pode provocar alterações comportamentais e fazer com que alguns peixes evitem a aproximação, enquanto outros sejam atraídos (DI FRANCO; BAIATA; MILAZZO, 2013; EMSLIE et al., 2018; HUDDART, 2019). Entretanto, essa plasticidade comportamental varia de espécie para espécie. Apesar do avanço no conhecimento sobre estes efeitos, os impactos sobre peixes recifais intimamente associados ao habitat (e.g. espécies territoriais) têm recebido pouca atenção. Estes indivíduos alcançam seus diferentes estágios de desenvolvimento nos recifes, pois encontram alimento e proteção necessários para sobrevivência (FRÉDÉRICH; PARMENTIER, 2016). Por isso, exibem limitada mobilidade entre habitats e podem não conseguir escapar de ambientes estressados pela presença humana.

Peixes territoriais, como os peixes-donzela ou donzelinhas (Pomacentridae), são espécies-chave em ecossistemas marinhos. Além de implacáveis defensores territoriais, mantêm um notável cultivo de algas, influenciando na abundância das comunidades bentônicas e na dinâmica de peixes herbívoros errantes nos recifes de coral (CECCARELLI; JONES; MCCOOK, 2001; JONES et al., 2006). Para estes peixes, identificar uma ameaça é crucial para evitar gastos energéticos desnecessários com a defesa do território, evitando assim, prejuízos à sua aptidão física (e.g. diminuição nas taxas de forrageamento, crescimento e reprodução) (FRÉDÉRICH; PARMENTIER, 2016). Portanto, a intimidação do homem no ambiente recifal (mesmo sem o efeito letal) pode representar um distúrbio adicional para os peixes territoriais, que devem ser capazes de equilibrar entre assumir o risco ou defender seus recursos de maneira eficiente. Consequentemente, podemos representar uma ameaça direta para a dinâmica das espécies marinhas e a resiliência do ambiente recifal.

Lidar com o efeito cumulativo da exposição à mergulhadores representa um potencial desafio para gestores dos recursos marinhos, os quais buscam garantir a coexistência entre animais silvestres e turistas (BURGIN; HARDIMAN, 2015; HUDDART, 2019). Dessa forma, compreender a variedade de respostas dos peixes

territoriais aos distúrbios ligados a presença humana pode contribuir com o planejamento de intervenções direcionas às atividades de mergulho (i.e., que minimizem os efeitos nocivos diretos e indiretos à vida marinha). Além disso, deve ampliar o conhecimento sobre as relações entre predador-presa e expandir o conceito da paisagem marinha do medo.

Nesta tese, explorei os impactos da presença humana no comportamento de peixes territoriais seguindo três distintos, porém complementares, caminhos. No primeiro capítulo, comparei se a presença de mergulhadores, com equipamento SCUBA e em mergulho livre, pode causar medo e alterar a territorialidade da donzelinha *Stegastes fuscus* (Cuvier, 1830) em Arraial do Cabo - RJ, um dos destinos de mergulho mais visitados do Brasil. No segundo capítulo, investiguei a relação entre a percepção do risco com a abordagem do mergulhador livre, e o tempo destinado ao comportamento territorial de duas espécies de donzelinhas, *Stegastes apicalis* (De Vis, 1885) e *Pomacentrus wardi* Whitley, 1927*,* comuns em águas rasas na Grande Barreira de Corais, Austrália. No terceiro capítulo, examinei se a donzelinha *Stegastes sanctipauli* Lubbock & Edwards, 1981 distingue a percepção do risco entre um modelo do predador *Sphyraena barracuda* Walbaum, 1792 e abordagem do mergulhador, no menor arquipélago do Atlântico Equatorial, Arquipélago de São Pedro e São Paulo. Neste mesmo capítulo, para ter uma visão ampla dos padrões comportamentais em resposta aos efeitos não-letais da presença humana, comparei a atividade de forrageamento das quatro espécies de donzelinhas estudadas nesta tese sob o distúrbio do mergulhador, em três sistemas recifais distintos: recife em ilha remota não aberta ao turismo, recife costeiro aberto ao turismo e recife em ilha continental aberta ao turismo.

Referências

BARKER, N. H. L. L.; ROBERTS, C. M. Scuba diver behaviour and the management of diving impacts on coral reefs. **Biological Conservation**, v. 120, n. 4, p. 481–489, dez. 2004.

BARNETT, A. et al. Ecotourism increases the field metabolic rate of whitetip reef sharks. **Biological Conservation**, v. 199, p. 132–136, 2016.

BENEVIDES, L. J. et al. Fish escape behavior as a monitoring tool in the largest

Brazilian multiple-use Marine Protected Area. **Ocean & Coastal Management**, v. 152, n. November 2017, p. 154–162, fev. 2018.

BLUMSTEIN, D. T. et al. Testing a key assumption of wildlife buffer zones: Is flight initiation distance a species-specific trait? **Biological Conservation**, v. 110, n. 1, p. 97–100, 2003.

BURGIN, S.; HARDIMAN, N. Effects of non-consumptive wildlife-oriented tourism on marine species and prospects for their sustainable management. **Journal of Environmental Management**, v. 151, p. 210–220, 2015.

CECCARELLI, D. M.; JONES, G. P.; MCCOOK, L. J. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. In: TAYLOR & FRANCIS (Ed.). **Oceanography and Marine Biology: An Annual Review**. 1st Editio ed. London: CRC Press, 2001. v. 39p. 355–389.

CIUTI, S. et al. Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. **PLoS ONE**, v. 7, n. 11, 2012.

CLINCHY, M. et al. Fear of the human “super predator” far exceeds the fear of large carnivores in a model mesocarnivore. **Behavioral Ecology**, v. 00, p. arw117, 2016.

DARIMONT, C. T. et al. The unique ecology of human predators. **Science**, v. 349, n. 6250, p. 858–860, 2015.

DI FRANCO, A. et al. Scuba diver behaviour and its effects on the biota of a Mediterranean marine protected area. **Environmental Conservation**, v. 36, n. 01, p. 32, 9 abr. 2009.

DI FRANCO, A.; BAIATA, P.; MILAZZO, M. Effects of recreational scuba diving on mediterranean fishes: Evidence of involuntary feeding? **Mediterranean Marine Science**, v. 14, n. 1, p. 15–18, 2013.

EMSLIE, M. J. et al. Reef fish communities are spooked by scuba surveys and may take hours to recover. **PeerJ**, v. 6, p. e4886, 24 maio 2018.

FRÉDÉRICH, B.; PARMENTIER, E. **Biology of damselfishes**. [s.l.] CRC Press, Taylor & Francis, 2016.

FRID, A.; DILL, L. Human-caused Disturbance Stimuli as a Form of Predation Risk. **Conservation Ecology**, v. 6, n. 1, p. 1–12, 2002.

GIGLIO, V. J. et al. Using an educational video-briefing to mitigate the ecological impacts of scuba diving. **Journal of Sustainable Tourism**, v. 9582, n. December, p. 1–16, 2017.

GIGLIO, V. J. et al. Scuba diving and sedentary fish watching : effects of photographer approach on seahorse behavior. **Journal of Ecotourism**, v. 0, n. 0, p. 1–10, 2018.

GIGLIO, V. J.; LUIZ, O. J.; FERREIRA, C. E. L. Ecological impacts and management strategies for recreational diving : A review. **Journal of Environmental Management**, v. 256, n. February 2019, p. 109949, 2020.

GIL, M. A. et al. Rapid tourism growth and declining coral reefs in Akumal, Mexico. **Marine Biology**, v. 162, n. 11, p. 2225–2233, 23 nov. 2015.

HASLER, H.; OTT, J. A. Diving down the reefs? Intensive diving tourism threatens the reefs of the northern Red Sea. **Marine pollution bulletin**, v. 56, n. 10, p. 1788–94, out. 2008.

HAWKINS, J. P. et al. Effects of recreational scuba diving on caribbean coral and fish communities. **Conservation Biology**, v. 13, n. 4, p. 888–897, 1999.

HUDDART, D. Recreational Scuba Diving and Snorkelling. In: HUDDART, D.; STOTT, T. (Eds.). **Outdoor Recreation**. 1st. ed. Cham, Switzerland: Springer International Publishing, 2019. p. 361–394.

JANUCHOWSKI-HARTLEY, F. A. et al. Fear of fishers: human predation explains behavioral changes in coral reef fishes. **PLoS ONE**, v. 6, n. 8, p. e22761, 10 ago. 2011.

JONES, G. P. G. et al. Resource use and impact of three herbivorous damselfishes on coral reef communities. **Marine Ecology Progress Series**, v. 328, n. 2001, p. 215–224, 2006.

LAUNDRE, J. W.; HERNANDEZ, L.; RIPPLE, W. J. The Landscape of Fear: Ecological Implications of Being Afraid. **The Open Ecology Journal**, v. 3, n. 3, p. 1–7, 5 mar. 2010.

MADIN, E. M. P. et al. Human activities change marine ecosystems by altering predation risk. **Global Change Biology**, v. 22, n. 1, p. 44–60, jan. 2016.

NUNES, J. A. C. C. et al. Global trends on reef fishes' ecology of fear: Flight initiation distance for conservation. **Marine Environmental Research**, v. 136, n. November 2017, p. 153–157, maio 2018.

ROCHE, R. C. et al. Recreational Diving Impacts on Coral Reefs and the Adoption of Environmentally Responsible Practices within the SCUBA Diving Industry. **Environmental Management**, v. 58, n. 1, p. 107–116, 7 jul. 2016.

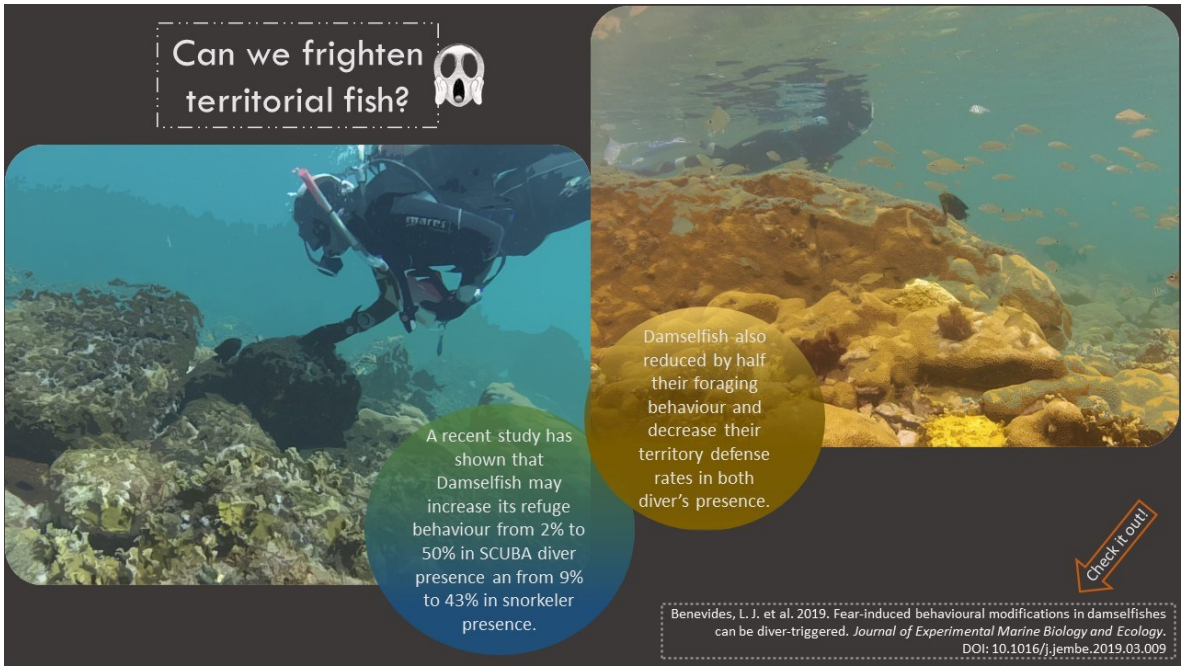
SAMIA, D. S. M. et al. A meta-analysis of fish behavioural reaction to underwater human presence. **Fish and Fisheries**, n. September 2018, p. 1–13, 2019.

TITUS, B. M.; DALY, M.; EXTON, D. A. Do reef fish habituate to diver presence? Evidence from two reef sites with contrasting historical levels of SCUBA intensity in the Bay islands, Honduras. **PLOS ONE**, v. 10, n. 3, p. e0119645, 25 mar. 2015.

II. FEAR-INDUCED BEHAVIOURAL MODIFICATIONS IN DAMSELFISHES CAN BE DIVER-TRIGGERED

Larissa J. Benevides, Gabriel C. Cardozo-Ferreira, Carlos Eduardo L. Ferreira, Pedro Henrique C. Pereira, Taciana K. Pinto & Cláudio Luis S. Sampaio

Press release



Artigo publicado na revista *Journal of Experimental Marine Biology and Ecology*

Fear-induced behavioural modifications in damselfishes can be diver-triggered

Larissa J. Benevides[a,*], Gabriel C. Cardozo-Ferreira[b], Carlos Eduardo L. Ferreira[c], Pedro Henrique C. Pereira[d], Taciana K. Pinto[e], Cláudio Luis S. Sampaio[f]

[a] *Programa de Pós-graduação em Diversidade Biológica e Conservação nos Trópicos, ICBS, Universidade Federal de Alagoas (UFAL), Maceió, Alagoas, Brazil*
[b] *Laboratório de Ictiologia, Departamento de Oceanografia e Ecologia, Universidade Federal Espírito Santo (UFES), Vitória, Espírito Santo, Brazil*
[c] *Laboratório de Ecologia e Conservação de Ambientes Recifais (LECAR), Departamento de Biologia Marinha, Universidade Federal Fluminense (UFF), Niterói, RJ, Brazil*
[d] *Departamento de Oceanografia, CTG, Universidade Federal de Pernambuco (UFPE), Cidade Universitária, Recife, PE, Brazil*
[e] *Laboratório de Ecologia Bentônica, U. E. Penedo, Campus Arapiraca, Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, ICBS, Universidade Federal de Alagoas (UFAL), Penedo, Alagoas, Brazil*
[f] *Laboratório de Ictiologia e Conservação, U. E. Penedo, Campus Arapiraca, Programa de Pós-graduação em Diversidade Biológica e Conservação nos Trópicos, ICBS, Universidade Federal de Alagoas (UFAL), Maceió, Alagoas, Brazil*

ARTICLE INFO

Keywords:
Diver disturbance
Fish behaviour
Stegastes fuscus
Territoriality

ABSTRACT

Fear is a short-term response arisen from the way an animal perceives its environment when some threat makes it insecure. Thus, the risk perception of predation shapes the cost-benefit decisions associated with food and safety in animal communities. Even non-consumptive human-related activities such as ecotourism may influence species behavioural traits. Marine wildlife tourism might produce different impacts on organisms, stressing and modifying (directly or indirectly) species behaviour, physiology and habitat use. Understand the effects of human presence on site-attached fish' behaviour is crucial to elucidate how dive-tourism could shape their limited-range seascape. Given the importance of the territorial damselfishes as reef farmers and 'ecosystems engineers', here we investigated if the presence of SCUBA divers and snorkelers can disrupt the foraging and territorial defence of the Dusky damselfish, *Stegastes fuscus*. Experimental approaches (diver presence and absence) were applied in 30 territories of *S. fuscus* using underwater remote video cameras. Behavioural responses were analysed by considering the frequency of refuge, foraging and chase behaviours. Both recreational dive activities had an analogous role in frighten and disturb the Dusky damselfish activities. Considering the frequency of behaviours displayed in diver's absence vs presence, *S. fuscus* increased its refuge times from approximately 2% to 50% on SCUBA diver presence and from 9% to 43% in snorkeler presence. It is directly linked to the missed feeding opportunities, which reduced by half during both diver's presence. Damselfish's aggressiveness proportionally dropped (0.3%) during SCUBA diver presence but increased (2.4%) while snorkeler was present. However, the average frequency of chase behaviour reduced with both divers' approach. Interruptions in damselfish behaviour may modify the resource monopolization and productivity inside their territories, affecting its relationships with other species beyond the boundaries of their territoriality, and leading a possible change on its functional role in the reef community. Territorial reef fish behaviour and their relationship with divers' presence can provide a more holistic comprehension regarding the seascape of fear concept and could be useful as an indicator of human disturbances.

1. Introduction

The "landscape of fear" (LOF) is a well-grounded concept modelled to explain the fear-driven spatial pattern of habitat use and the behavioural outcome of predator-prey interactions in terrestrial and marine ecosystems (Gallagher et al., 2017; Laundré et al., 2010). In marine systems, the "seascape of fear" has been applied to mammals and sea turtles, which tend to decrease their use of high-quality foraging habitats in predators' presence (Heithaus et al., 2007; Wirsing et al., 2008). Likewise, the non-consumptive effect of predators (i.e. *risk-effect,* or the behavioural outcome of prey to predators' presence) has been demonstrated to alter herbivory and the small-scale distribution

* Corresponding author.
E-mail addresses: benevideslai@gmail.com (L.J. Benevides), gabrielccf@gmail.com (G.C. Cardozo-Ferreira), carlosferreira@id.uff.br (C.E.L. Ferreira), pedrohcp2@yahoo.com.br (P.H.C. Pereira), taciana@penedo.ufal.br (T.K. Pinto), claudio.sampaio@penedo.ufal.br (C.L.S. Sampaio).

https://doi.org/10.1016/j.jembe.2019.03.009
Received 4 December 2018; Received in revised form 19 March 2019; Accepted 20 March 2019

patterns of prey in higher risk areas (Catano et al., 2016; Matassa and Trussell, 2011). Nevertheless, while the LOF concept has emerged having in mind the natural predator effect, it is essential to consider the fear-induced by human presence on prey' landscape/seascape, once humans have a competitive dominance over predators' population and predatory behaviour during hunting or fishing activities (Darimont et al., 2015; Madin et al., 2016).

The fear generated by exploratory activities may lead wild animals to perceive humans as a predator (Frid and Dill, 2002) or even more threatening than a natural predator (Ciuti et al., 2012; Clinchy et al., 2016). The human threat to marine ecosystems has been historically reported as a result of the direct *lethal effect* of predators harvesting (e.g. reducing predator abundance and biomass) (Heithaus et al., 2008; Jackson et al., 2001). However, the *risk effect* of human activity can also alter the seascape by modifying the perception of predation risk, influencing prey behavioural traits (Madin et al., 2016). For instance, even in ecotourism activities (commonly known as a low impact), humans can influence species activities dictating when, where or what the prey eats, affecting metabolic rates and communities' structure (Albuquerque et al., 2015; Barnett et al., 2016; Burgin and Hardiman, 2015).

Marine wildlife tourism (MWT), defined as tourism of observing and/or interacting with marine species in their natural environment, is a common activity often centred in providing viable economic opportunities for local communities (Burgin and Hardiman, 2015; Trave et al., 2017). Accordingly, it offers support for conservation and unique marine experiences, such as shark and whale encounter or shipwreck SCUBA diving (Trave et al., 2017). On the other hand, MWT is widely recognized to stress and modify directly or indirectly species behaviour/physiology as well as habitat use (Burgin and Hardiman, 2015; Lusseau, 2004; Rizzari et al., 2017). Therefore, the MWT impacts include physical damages on benthic organisms (Giglio et al., 2017; Giglio et al., 2016), behavioural disturbances in focal and non-focal species (Giglio et al., 2018; Rizzari et al., 2017), increase on stress and metabolic rates, and reduction on antipredator responses' learning due to boat noise traffic (Ferrari et al., 2018; Nedelec et al., 2017; Simpson et al., 2016) and food provisioning (Barnett et al., 2016). On highly mobile fishes, such as herbivorous, the threat of human presence in touristic areas has demonstrated to affect wariness (Benevides et al., 2018), abundance and assemblage structure (Albuquerque et al., 2015; Gil et al., 2015). Yet, the fear effect of MWT has been poorly tested in site-attached fishes and its importance could be currently underestimated.

Site-attached individuals may be unable to move away from stressed environments and since they have a limited range of movement, human-related activities could have a stronger pressure on those species. For example, reef dweller fishes must constantly make trade-off decisions to avoid potential fitness impairment (e.g. decrease in foraging, growth and reproduction rates) due to the risk perception of human approach, as observed for fishes associated with coral colonies (Pereira et al., 2016). In consequence, they spend more time closer or hiding within the coral branches, and decreases the swimming activity with diver's approach (Pereira et al., 2016). Despite the relevant evidence of diver influence on fish behaviour (Emslie et al., 2018; Titus et al., 2015; Watson and Harvey, 2007), we still have a poor comprehension regarding the fear induced by diver presence and its consequences on territorial fish's habitat use. This would increase the insights into the cumulative effect of repeated diver exposure on marine ecosystem function, moving beyond the understanding of the predator-prey relationship and expanding, even more, the seascape of fear models, since this concept has not yet been applied for a fish species spatially dependent. In addition, it would help conservation managers to make more appropriated interventions in diving destinations.

Between territorial fishes, damselfishes (Pomacentridae) are one of the most abundant and ecologically important on coral reefs (Ceccarelli et al., 2001, 2005). By defending their territories, these fishes display evident aggressiveness towards potential intruders and/or competitors (Leal et al., 2015; Osório et al., 2006; Souza et al., 2011). Herbivory and weeding behaviour by damselfishes can modify diversity and biomass of algae and associated cryptofauna inside their territories, beyond increasing the productivity of the whole coral reef system (Ferreira et al., 1998; Hixon and Brostoff, 1983). Thus, these fishes represent an important ecological model to detect impacts on marine systems modulated by natural or anthropogenic stressors.

The present study aimed to investigate whether the presence of SCUBA divers and snorkelers can scare and disrupt the territoriality of the Dusky damselfish, *Stegastes fuscus* (Cuvier, 1830). *S. fuscus* is among the most common and aggressive species of the Pomacentridae family in the Brazilian coast. This species is abundant on coral colonies, algal, and rocky reefs (Leal et al., 2013; Medeiros et al., 2010; Osório et al., 2006) and display major influence over the benthic and fish assemblages (Ferreira et al., 1998; Osório et al., 2006). Here we tested the hypothesis that the diver's presence can modify *S. fuscus* individuals' behaviour, reducing their foraging and chase activities and increasing the frequency of refuge use.

2. Material and methods

2.1. Study area

Popularly known as the "Brazilian diving capital", the region of Arraial do Cabo, in the state of Rio de Janeiro, represent one of the most visited dive sites in Brazil, especially along the south-eastern coast (Giglio et al., 2017). Among the motivations for diving tourism, Arraial do Cabo highlights as a marine biodiversity hotspot in the South-western Atlantic, having one of the richest reef fish fauna of Brazilian coastal reefs (Ferreira et al., 2004; Floeter et al., 2001). This is favoured by the combining subtropical and warm-temperature habitats, with more exposed rocky shores seasonally bathed by upwelling events, and sheltered ones with tropical/subtropical conditions (Cordeiro et al., 2016). At least 13 SCUBA diving companies operate in the Arraial do Cabo Marine Extractive Reserve (ACMER), performing approximately 25.000 dives per year (Giglio et al., 2017). Beyond that, there are numerous nautical tourism boats serving snorkelers or visitors that only want sail between the small inlets. The ACMER was established as a sustainable use marine protected area in 1997 and despite the existence of commercial, recreational fishing and tourism zones and specific management rules, there is poor enforcement of environmental regulations and lack of no-take zones.

The study sites were selected based on intensity and type of recreational diving activities. Therefore, fish behaviour was assessed in two popular dive sites namely Forno (22°58′6.13"S, 42° 0'56.53"W), and Anequim (22°58′52.34"S, 41°59′3.43"W), which has as main activities snorkeling and SCUBA diving, respectively. At Forno, the benthos coverage is mainly composed by cnidarians (i.e. scleractinians, hydrocorals, zoanthids and octocorals), especially the zoanthid *Palythoa caribeaorum,* and branching hydrocorals *Millepora alcicornis* (Rogers et al., 2014). Epilithic algal matrix (EAM) is the most predominant benthic group at Anequim, followed by *M. alcicornis* in shallow and *P. caribeaorum* in deeper areas (> 9 m) (Giglio et al., 2017). These rock reef's cover in ACMER suggest this area as having less structural complexity and coral cover than at many coral reef dive destinations (Giglio et al., 2017). The former area is a mainland inlet, having access by land, diving or nautical tourism boats, whereas the latter one is located on a coastal island being the access only possible through diving or nautical tourism boats.

2.2. Data collection

Data were obtained in March 2017 at sheltered inshore rocky reefs, at depths between 1 m and 5 m. We randomly selected 15 territories of *S. fuscus* adults in each study site/dive activity (Snorkel at Forno beach

and SCUBA at Anequim), totalling 30 territories separated from each other by at least 4 m. All observations were gathered between 10 am and 3 pm due to the visibility conditions. Fish size was visually estimated and ranged between 11 cm and 13 cm total length and individuals with nests in their territories were excluded from analysis. In each territory, we applied two distinct experimental approaches: Control (C) – without diver presence, and Treatment (T) – with a stimulus of a diver.

In order to record *S. fuscus* behaviour in both experimental approaches, remote underwater video cameras were attached to dive weights and deployed on the seafloor at a distance of 1.0 m – 1.5 m from the Dusky damselfish territories. The territories were defined after a prior observation of the *S. fuscus* swimming, foraging and/or aggressive activity. One video camera was used in each territory to avoid further interference. After deployed, the camera was left recording for 20 min without interruption of any diver. Tourists that tried getting closer were warned to stay far to not interfere with the research. After this time, the research diver returned and then started the T, swimming around the damselfish territory (i.e. swimming above, or at same depth; swimming a little bit far and then close again) and simulating diver tourist behaviour (e.g. sometimes looking closer and/or trying to touch the fish) during 15 min.

In preliminary trials, it was observed that shifts in fish individual's behaviour could be caused by diver disturbance while deploying the camera. Consequently, it was assumed an acclimation period of fish between 3 and 5 min. Hence, the initial 5 min of each video from the control analysis were excluded.

2.3. Data analysis

All recorded videos were analysed in the Behavioural Observation Research Interactive Software – BORIS (Friard and Gamba, 2016), where were computed the frequency (number of times/recording minutes) of the following behaviours by individual focus: aggressiveness against other fishes (chasing behaviour), refuge (hiding in a shelter structure) and foraging (bites on the substrate).

In order to compare the behavioural responses of *S. fuscus* between C vs T, a repeated measures permutational multivariate analysis of variance (PERMANOVA) was calculated for each dive activity (snorkel and SCUBA), separately. It was based on 999 permutations, a binomial deviance resemblance matrix and on the design: 'experimental approach' as a fixed factor with two levels (C vs T). A repeated-measure was used because the samples are not independent (Anderson et al., 2008). Both experimental approaches (control and treatment) of the field experiment was conducted at the same individual and replicated in 30 individuals. In addition, a principal component analysis (PCA) was performed using 'FactorMineR' package (Lê et al., 2008) to summarize the datasets and investigate which behaviour could have more influence in describing the experimental approaches applied in each dive activity. Ellipses (CI = 95%) were drawn for each category (C and T) in each dive activity around the mean distance of each sample to the centroid over the PCA points.

Repeated measures PERMANOVA were performed in Primer 6+ (Anderson et al., 2008). PCA and all plots were conducted in R software (R Core Team, 2017). A significance level of $\alpha < 0.05$ was considered in all analysis.

3. Results

The effect of snorkel and SCUBA diver disturbance on *Stegastes fuscus* behaviour.

The influence of snorkeler was analogous to the SCUBA diver in affecting the *S. fuscus* behaviour. For both dive activities, when in the diver presence (T), *S. fuscus* chased the intruders away and foraged on substrate less frequently, and spent more time seeking refuge (Mean ± S.D.; SCUBA diver presence: chase = 0.53 ± 1.13; bites = 13.20 ± 7.92; refuge = 13.87 ± 6.3/Snorkeler presence: chase = 3.87 ± 5.62; bites = 10.87 ± 11.03; refuge = 10.93 ± 8.66) than in diver absence (C) (Mean ± S.D.; SCUBA diver absence: chase = 1 ± 1.07; bites = 43.53 ± 20.97; refuge = 0.93 ± 1.39/ Snorkeler absence: chase = 5.13 ± 5.68; bites = 31.80 ± 20.49; refuge = 3.47 ± 8.46) (Fig. 1).

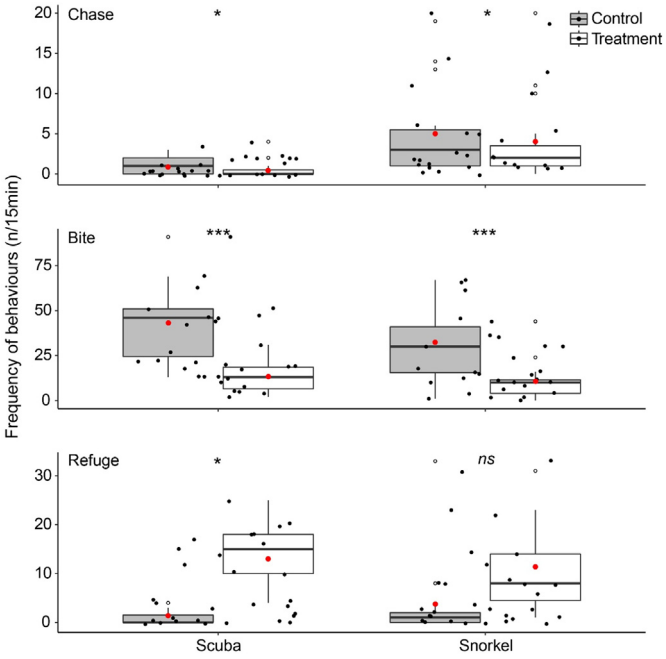


Fig. 1. Comparative behaviour performed by replicated *S. fuscus* individuals between the experimental approaches (Control vs Treatment – grey and white boxes, respectively) in each dive activity (SCUBA and snorkel). Values are the frequency of behavioural displays counts during 15 min. Boxes indicate 25th and 75th quantiles, the central line in the box is the median, whiskers are the Standard Error (the minimum and maximum distribution values) of the behaviour's frequency. Red dots represent mean values. ° = outliers. * indicate significance level: * < 0.05; ** < 0.01; *** < 0.001. *ns*: non-significant result from PERMANOVA for the comparisons between C and T. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

When the snorkeler stimulus was tested, significant differences between C and T were found for the frequencies of chase (PERMANOVA: Pseudo-$F = 7.590$, $p = 0.02$) and bites (Pseudo-$F = 18.562$, $p = 0.001$). However, there were no differences in the frequency of refuge rates (Pseudo-$F = 1.564$, $p = 0.236$) (Fig. 1). For SCUBA diver stimulus, differences were found in the three behavioural displays tested between C and T: chase (Pseudo-$F = 171.41$, $p = 0.013$), bites (Pseudo-F = 444.45, $p = 0.001$) and refuge (Pseudo-$F = 46.308$, $p = 0.011$) (Fig. 1).

Behavioural changes to snorkeler stimulus explain 78.72% of the total variability on data in the first two axes of PCA results (Fig. 2). An evident separation can be observed between C and T, where biting and refuge behaviours were the main responsible for data distribution in opposite directions on Dim. 1 (PCA eigenvalues: chase = 0.676, bites = −0.735, refuge = 0.771). Chasing behaviour was the main responsible for data distribution on Dim. 2 (PCA eigenvalues: chase = 0.718, bites = 0.472, refuge = −0.179) (Fig. 2).

Regarding the SCUBA diver stimulus, behavioural changes explain 82.57% of the total variability on data distribution in the first two axes of PCA. A separation between C and T was also observed. Biting behaviour influenced most of data distribution on Dim. 1 (PCA eigenvalues: chase = 0.524, bites = 0.833, refuge = −0.787), while chasing behaviour was the main responsible on Dim. 2 (PCA eigenvalues: chase = 0.844, bites = −0.164, refuge = 0.388) (Fig. 3).

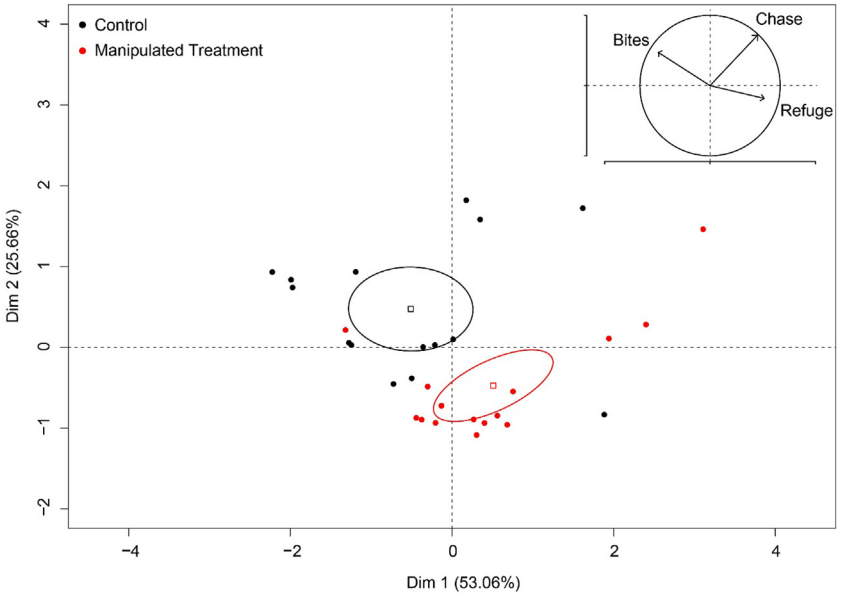


Fig. 2. Principal Components Analysis (PCA) results of *Stegastes fuscus* behaviours comparative between Control and Treatment to the snorkeler stimulus. Vectors represent the trends (direction and importance) of each behaviour. Ellipses are 95% confidence intervals around the mean of the sample's distribution for each category of experimental approaches.

4. Discussion

Behavioural changes of *S. fuscus* individuals indicated that this species has set some level of apprehension from the closest approach of a diver, refuging in holes or crevices and reducing but not ceasing its aggressiveness and foraging. Feeding opportunities were missed by the direct influence of divers' presence, either by snorkeling or by SCUBA diving. Thereby, our findings demonstrated that both dive activities play an analogous role, disrupting the Dusky damselfish behaviours and influencing its territory defence.

Reduction in *S. fuscus* foraging activity and an increase on refuge use express an antipredator (or vigilant) response to the diver stimulus. Economic models of refuge use predict that hiding in a refuge increase safety but often incur fitness costs for an individual or overall survival of a population (e.g. due the loss of time to foraging or loss of mating opportunities) (Cooper and Blumstein, 2015). Given that damselfishes are important ecosystem engineers (Jones et al., 2012), a suboptimal hiding decision of *S. fuscus* could either lead them to starvation or drive negative consequences towards its community.

For example, the most evident impact of damselfishes' behaviour is over benthic algal assemblages within their territories, which is distinct regarding algal biomass, productivity (Ferreira et al., 1998), nitrogen fixation (Russ, 1987), species composition, diversity and successional patterns (Hixon and Brostoff, 1996). These differences between territories and surrounding areas may affect the density of cryptofaunal communities (small invertebrates) by creating refuges or enhancing food supplies, and local distribution of herbivorous fishes and invertebrates (e.g. sea urchins) (Ceccarelli et al., 2001; Ferreira et al., 1998; Hixon and Brostoff, 1996). As a result, the short-term behavioural changes caused by the 'fear effect' of a diver may lead to overall disturbances beyond the boundaries of their territories. Thus, this trend could have a strong influence on the species habitat use, competition and fitness, affecting the damselfish functional role on coral reefs.

In general, fish that live strongly associated with the habitat

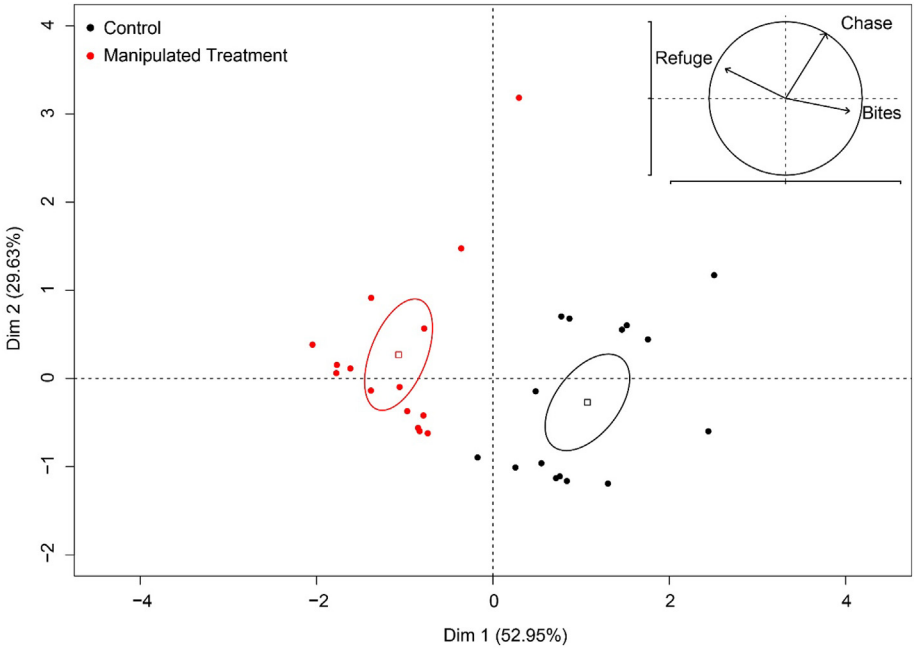


Fig. 3. Principal Components Analysis (PCA) results of *Stegastes fuscus* behaviour comparative between Control and Treatment to the SCUBA diver stimulus. Vectors represent the trends (direction and importance) of each behaviour. Ellipses are 95% confidence intervals around the mean of the sample's distribution for each category of experimental approaches.

structure for settle, shelter or food may benefit of reducing encounter rates with predators and change its safety perception according to the coral complexity (e.g. the branch spacing and size) (Almany, 2004; Noonan et al., 2012; Pereira and Munday, 2016). For instance, the topographic complexity can alter how damselfish individuals assess the risk from an approaching threat, shifting from visual assessments to olfactory cues and balancing between fitness related activities, like foraging, in behalf of increasing the vigilance (McCormick and Löonnstedt, 2013). Here, we did not estimate the habitat complexity of the surveyed territories. Notwithstanding, take into account the territory complexity of damselfish could enlighten how the cost-benefit decisions to hiding from a diver are correlated to the habitat heterogeneity, and whether it could shape the fish's antipredator behaviour in a higher coral cover area, where the diving industry is commonly attracted.

Changes in animal behaviour related to human impacts can improve individuals' likelihood to cope in altered environmental conditions and survive (Wong and Candolin, 2015). Nonetheless, human-related activities, especially in coastal zones, have been exposing many reef-associated species to more than one stressor simultaneously (Hughes and Connell, 1999). This process contributes to a decrease in species adaptation success rates and increases severe fitness consequences (Tuomainen and Candolin, 2011; Wong and Candolin, 2015). As an example, coral reefs have been affected by global (climate change) and local (pollution and fishing) stressors (Johansen and Jones, 2011; Rummer and Munday, 2017; Sih et al., 2011; Zaneveld et al., 2016), which have been driving a reduction on reef resilience and decreasing ecosystem functioning (Bellwood et al., 2004; Ruppert et al., 2018). Considering that any reef exposed to human activity is vulnerable to at least one of those stressors, in touristic areas the diver's presence adds another stressful source for disrupt reef fish behaviour and reduce their ability to recover from a prior synergism of impacts.

Contrary to our results, Geffroy et al. (2015) have suggested that human presence in a nature-based tourism area can temporary lighten the antipredator behaviour of an individual (e.g. during summer tourism seasons), creating a 'human shield' syndrome as a result of habituation. Both habituation and sensitization to human presence occur over time and is related to different degrees of tolerance to a stimulus exposure (Bejder et al., 2009). Although we have measured the behavioural changes at a single point in time, not over a repeated or continuous exposure, the damselfish tolerance level did not tend to increase during the entire observation time with diver presence. Therefore, our behavioural observations provided one piece of evidence that habituation to diver presence may not occur in territorial fishes that inhabit high tourist visiting areas. Still, experimental designs testing an ongoing diver stimulus on the same individual through time will better able to detect fish responsiveness to a diving tourism routine of disturbance.

To assess how anthropogenic stressors have been affecting coral reefs, many reefs monitoring programs remain focused to include information about abundance and length of key indicators species (Hodgson, 2000; Lang et al., 2010). However, a different database including species behaviour could be much more useful in providing information related to human impact on reef ecosystems. Understand the behavioural responses of site-attached species to frequent human disturbance can play a pivotal role in precede management interventions before demographic response become evident (Greggor et al., 2016). Despite the lack of efficient communication between research and management actions, evidence for the effectiveness of animal behaviour as a conservation tool has been growing and stimulating by demonstrating how behaviour is a powerful indicator of the anthropogenic impact on marine ecosystems (Berger-Tal et al., 2016; Blackwell et al., 2016; Greggor et al., 2016).

Our findings demonstrated that diver presence might disrupt damselfish' functions and its influence on other species that are likely to alter territorial reef fishes ecological role. Future research questions could be focused on testing a chronic effect (i.e. a persistent alteration) of how fear-induced behavioural changes driven by divers over site-attached fishes could influence the ecological role of this species on a coral reef, including long-term measurements of territorial fish ecology (e.g., the quantity and quality of food algae inside the territory, or the success in nest defence).

Considering management initiatives, a rigorous monitoring plan to dive-tourism activities should include the time of diving trips and the number of divers per trip. We demonstrated herein that the time of diver stimulus had effects on fish behaviour. Consequently, amplifying this disturbance to a 30 min or 1-h diving trip with more than one diver, could have a huge impact in territorial fish's behaviours. In addition, we suggest for a further study the evaluation of a minimum distance in which the diver could approach the marine animals without disrupting their behaviour (e.g. 1, 2 or 3 m), especially to site-attached organisms such as territorial fishes. It was observed during our fieldwork as a potential variable to reduce the effects of the fish vulnerability to human disturbances. In turn, it will improve the tourist's perceptions about having a responsible behaviour and conservation awareness while enjoying the contact with the marine environment.

In summary, our study shows that interruptions in damselfish behaviour due to the diver's effect may modify its frequency in foraging and territory defence. Since individuals living in a reef dominated by human activities weigh diver's presence in their cost-benefit decisions, behavioural modifications can be used as an indicator of disturbances. Besides, these behavioural responses provide a more holistic comprehension of the seascape of fear concept, including the effect of 'human as a predator' on the manner in which territorial fish use their reef-scape.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2019.03.009.

Acknowledgements

We thank J-C Joyeux for the valuable comments on the manuscript. Reef Systems Ecology and Conservation Lab (www.lecar.uff.br) gave logistic support. LJB was supported by CAPES - Coordination for the Improvement of Higher Education. GCCF is supported by FAPES – Foundation for research support of Espírito Santo State. CELF is supported by grants from CNPq, FAPERJ and FUNBIO.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

Albuquerque, T., Loiola, M., Nunes, J. de A.C.C., Reis-Filho, J.A., Sampaio, C.L.S., Leduc, A.O.H.C., 2015. In situ effects of human disturbances on coral reef-fish assemblage structure: temporary and persisting changes are reflected as a result of intensive tourism. Mar. Freshw. Res. 66, 23. https://doi.org/10.1071/MF13185.

Almany, G.R., 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia 141, 105–113. https://doi.org/10.1007/s00442-004-1617-0.

Anderson, M., Gorley, R.N., Clarke, R.K., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods, in Plymouth: Plymouth Marine Laboratory. pp. 214.

Barnett, A., Payne, N.L., Semmens, J.M., Fitzpatrick, R., 2016. Ecotourism increases the field metabolic rate of whitetip reef sharks. Biol. Conserv. 199, 132–136. https://doi.org/10.1016/j.biocon.2016.05.009.

Bejder, L., Samuels, A., Whitehead, H., Finn, H., Allen, S., 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Mar. Ecol. Prog. Ser. 395, 177–185. https://doi.org/10.3354/meps07979.

Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. Nature 429, 827–833. https://doi.org/10.1038/nature02691.

Benevides, L.J., Pinto, T.K., Nunes, J. de A.C.C., Sampaio, C.L.S., 2018. Fish escape behavior as a monitoring tool in the largest Brazilian multiple-use marine protected area. Ocean Coast. Manag. 152, 154–162. https://doi.org/10.1016/j.ocecoaman.2017.11.029.

Berger-Tal, O., Blumstein, D.T., Carroll, S., Fisher, R.N., Mesnick, S.L., Owen, M.A., Saltz, D., St. Claire, C.C., Swaisgood, R.R., 2016. A systematic survey of the integration of animal behavior into conservation. Conserv. Biol. 30, 744–753. https://doi.org/10.1111/cobi.12654.

Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., Gese, E.M., Gilbert-Norton, L., Breck, S.W., 2016. No single solution: application of behavioural principles in mitigating human-wildlife conflict. Anim. Behav. 120, 245–254. https://doi.org/10.1016/j.anbehav.2016.07.013.

Burgin, S., Hardiman, N., 2015. Effects of non-consumptive wildlife-oriented tourism on marine species and prospects for their sustainable management. J. Environ. Manag. 151, 210–220. https://doi.org/10.1016/j.jenvman.2014.12.018.

Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W., Burkepile, D.E., 2016. Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. J. Anim. Ecol. 85, 146–156. https://doi.org/10.1111/1365-2656.12440.

Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2001. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 39, 355–389. https://doi.org/10.1016/j.chemphys.2005.03.003.

Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2005. Effects of territorial damselfish on an algal-dominated coastal coral reef. Coral Reefs 24, 606–620. https://doi.org/10.1007/s00338-005-0035-z.

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7. https://doi.org/10.1371/journal.pone.0050611.

Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., Macdonald, D.W., 2016. Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. Behav. Ecol. 00, arw117. https://doi.org/10.1093/beheco/arw117.

Cooper, W.E., Blumstein, D.T., 2015. Escaping from Predators: An Integrative View of Escape Decisions. United Kingdom, Cambridge.

Cordeiro, C.A.M.M., Mendes, T.C., Harborne, A.R., Ferreira, C.E.L., 2016. Spatial distribution of nominally herbivorous fishes across environmental gradients on Brazilian rocky reefs. J. Fish Biol. 89, 939–958. https://doi.org/10.1111/jfb.12849.

Darimont, C.T., Fox, C.H., Bryan, H.M., Reimchen, T.E., 2015. The unique ecology of human predators. Science 349, 858–860. https://doi.org/10.1126/science.aac4249.

Emslie, M.J., Cheal, A.J., MacNeil, M.A., Miller, I.R., Sweatman, H.P.A., 2018. Reef fish communities are spooked by scuba surveys and may take hours to recover. PeerJ 6, e4886. https://doi.org/10.7717/peerj.4886.

Ferrari, M.C.O., McCormick, M.I., Meekan, M.G., Simpson, S.D., Nedelec, S.L., Chivers, D.P., 2018. School is out on noisy reefs: the effect of boat noise on predator learning and survival of juvenile coral reef fishes. Proc. R. Soc. B Biol. Sci. 285. https://doi.org/10.1098/rspb.2018.0033.

Ferreira, C.E.L., Gonçalves, J.E.A., Coutinho, R., Peret, A.C., 1998. Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. J. Exp. Mar. Biol. Ecol. 229, 241–264. https://doi.org/10.1016/S0022-0981(98)00056-2.

Ferreira, C.E.L., Floeter, S.R., Gasparini, J.L., Ferreira, B.P., Joyeux, J.C., 2004. Trophic structure patterns of Brazilian reef shes: a latitudinal comparison. J. Biogeogr. 1093–1106. https://doi.org/10.1111/j.1365-2699.2004.01044.x.

Floeter, S.R., Guimaraes, R.Z.P., Rocha, L.A., Ferreira, C.E.L., Rangel, C.A., Gasparini, J.L., 2001. Geographic variation in reef-fish assemblages along the Brazilian coast. Glob. Ecol. Biogeogr. 10, 423–431. https://doi.org/10.1046/j.1466-822X.2001.00245.x.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7, 1325–1330. https://doi.org/10.1111/2041-210X.12584.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 1–12.

Gallagher, A.J., Creel, S., Wilson, R.P., Cooke, S.J., 2017. Energy landscapes and the landscape of fear. Trends Ecol. Evol. 32, 88–96. https://doi.org/10.1016/j.tree.2016.10.010.

Geffroy, B., Samia, D.S.M., Bessa, E., Blumstein, D.T., 2015. How nature-based tourism might increase prey vulnerability to predators. Trends Ecol. Evol. 30, 755–765. https://doi.org/10.1016/j.tree.2015.09.010.

Giglio, V.J., Luiz, O.J., Schiavetti, A., 2016. Recreational diver behavior and contacts with benthic organisms in the Abrolhos National Marine Park, Brazil. Environ. Manag. 57, 637–648. https://doi.org/10.1007/s00267-015-0628-4.

Giglio, V.J., Ternes, M.L.F., Mendes, T.C., Cordeiro, C.A.M.M., Ferreira, C.E.L., 2017. Anchoring damages to benthic organisms in a subtropical scuba dive hotspot. J. Coast. Conserv. 21, 311–316. https://doi.org/10.1007/s11852-017-0507-7.

Giglio, V.J., Ternes, M.L.F., Kassuga, A.D., Carlos, E.L., 2018. Scuba diving and sedentary fish watching: effects of photographer approach on seahorse behavior. J. Ecotourism 0, 1–10. https://doi.org/10.1080/14724049.2018.1490302.

Gil, M.A., Renfro, B., Figueroa-Zavala, B., Penié, I., Dunton, K.H., 2015. Rapid tourism growth and declining coral reefs in Akumal, Mexico. Mar. Biol. 162, 2225–2233. https://doi.org/10.1007/s00227-015-2748-z.

Greggor, A.L., Berger-Tal, O., Blumstein, D.T., Angeloni, L., Bessa-Gomes, C., Blackwell, B.F., St Clair, C.C., Crooks, K., de Silva, S., Fernández-Juricic, E., Goldenberg, S.Z., Mesnick, S.L., Owen, M., Price, C.J., Saltz, D., Schell, C.J., Suarez, A.V., Swaisgood, R.R., Winchell, C.S., Sutherland, W.J., 2016. Research priorities from animal behaviour for maximising conservation progress. Trends Ecol. Evol. 31, 953–964. https://doi.org/10.1016/j.tree.2016.09.001.

Heithaus, M.R., Frid, A., Wirsing, A.J., Dill, L.M., Fourqurean, J.W., Burkholder, D., Thomson, J., Bejder, L., 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. J. Anim. Ecol. 76, 837–844. https://doi.org/10.1111/j.1365-2656.2007.01260.x.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23, 202–210. https://doi.org/10.1016/j.tree.2008.01.003.

Hixon, M.A., Brostoff, W.N., 1983. Damselfish as a keystone in reverse: intermediate disturbance and diversity of reef algae. Science 220, 511–513.

Hixon, M.A., Brostoff, W.N., 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. Ecol. Monogr. 66, 67–90. https://doi.org/10.2307/2963481.

Hodgson, G., 2000. Coral Reef Monitoring and Management Using Reef Check. Reef Check Glob Surv Program. http://www.reefcheck.org/PDFs/ICZM.pdf.

Hughes, T.P., Connell, J.H., 1999. Multiple stressors on coral reefs: a long-term perspective. Limnol. Oceanogr. 44, 932–940. https://doi.org/10.4319/lo.1999.44.3_part_2.0932.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, Bruce J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Stenec, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 80 (293), 629–637. https://doi.org/10.1126/science.1059199.

Johansen, J.L., Jones, G.P., 2011. Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. Glob. Chang. Biol. 17, 2971–2979. https://doi.org/10.1111/j.1365-2486.2011.02436.x.

Jones, C.G., Lawton, J.H., Shachak, M., 2012. Organisms as ecosystem engineers. Oikos 69, 373–386. https://doi.org/10.2307/3545850.

Lang, J.C., Marks, K.W., Kramer, P.R., Ginsburg, R.N., 2010. AGRRA Protocols Version 5.4. http://www.agrra.org/coral-reef-monitoring/fish-indicator/.

Laundré, J.W., Hernandez, L., Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. Open Ecol. J. 3 (1–7). https://doi.org/10.2174/1874213001003030001.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25, 1–18. https://doi.org/10.18637/jss.v025.i01.

Leal, I.C.S., Pereira, P.H.C., De Araújo, M.E., 2013. Coral reef fish association and behaviour on the fire coral *Millepora* spp. in north-east Brazil. J. Mar. Biol. Assoc. UK. 93, 1703–1711. https://doi.org/10.1017/S0025315413000234.

Leal, I.C.S., de Araújo, M.E., da Cunha, S.R., Pereira, P.H.C., 2015. The influence of fire-coral colony size and agonistic behaviour of territorial damselfish on associated coral reef fish communities. Mar. Environ. Res. 108, 45–54. https://doi.org/10.1016/j.marenvres.2015.04.009.

Lusseau, D., 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. Ecol. Soc. 9, 1–15.

Madin, E.M.P., Dill, L.M., Ridlon, A.D., Heithaus, M.R., Warner, R.R., 2016. Human activities change marine ecosystems by altering predation risk. Glob. Chang. Biol. 22, 44–60. https://doi.org/10.1111/gcb.13083.

Matassa, C.M., Trussell, G.C., 2011. Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. Ecology 92, 2258–2266. https://doi.org/10.1890/11-0424.1.

McCormick, M.I., Löonnstedt, O.M., 2013. Degrading habitats and the effect of topographic complexity on risk assessment. Ecol. Evol. 3, 4221–4229. https://doi.org/10.1002/ece3.793.

Medeiros, P.R., Souza, A.T., Ilarri, M.I., 2010. Habitat use and behavioural ecology of the juveniles of two sympatric damselfishes (Actinopterygii: Pomacentridae) in the South-Western Atlantic Ocean. J. Fish Biol. 77, 1599–1615. https://doi.org/10.1111/j.1095-8649.2010.02795.x.

Nedelec, S.L., Radford, A.N., Pearl, L., Nedelec, B., McCormick, M.I., Meekan, M.G., Simpson, S.D., 2017. Motorboat noise impacts parental behaviour and offspring survival in a reef fish. Proc. R. Soc. B Biol. Sci. 284, 20170143. https://doi.org/10.1098/rspb.2017.0143.

Noonan, S.H.C., Jones, G.P., Pratchett, M.S., 2012. Coral size, health and structural complexity: effects on the ecology of a coral reef damselfish. Mar. Ecol. Prog. Ser. 456, 127–137. https://doi.org/10.3354/meps09687.

Osório, R., Rosa, I.L., Cabral, H., 2006. Territorial defence by the Brazilian damsel *Stegastes fuscus* (Teleostei: Pomacentridae). J. Fish Biol. 69, 233–242. https://doi.org/10.1111/j.1095-8649.2006.01095.x.

Pereira, P., Munday, P., 2016. Coral colony size and structure as determinants of habitat use and fitness of coral-dwelling fishes. Mar. Ecol. Prog. Ser. 553, 163–172. https://doi.org/10.3354/meps11745.

Pereira, P.H.C., Leal, I.C.S., de Araújo, M.E., 2016. Observer presence may alter the behaviour of reef fishes associated with coral colonies. Mar. Ecol. 37, 760–769. https://doi.org/10.1111/maec.12345.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. http://www.R-project.org/R Found Stat Comput Vienna, Austria.

Rizzari, J.R., Semmens, J.M., Fox, A., Huveneers, C., 2017. Observations of marine wildlife tourism effects on a non-focal species. J. Fish Biol. 91, 981–988. https://doi.org/10.1111/jfb.13389.

Rogers, R., de Oliveira Correal, G., de Oliveira, T.C., de Carvalho, L.L., Mazurek, P., Barbosa, J.E.F., Chequer, L., Domingos, T.F.S., de Andrade Jandre, K., Leão, L.S.D., de Andrade Moura, L., Occhioni, G.E., de Oliveira, V.M., Silva, E.S., Cardoso, A.M., de Castro e Costa, A., Ferreira, C.E.L., 2014. Coral health rapid assessment in marginal reef sites. Mar. Biol. Res. 10, 612–624. https://doi.org/10.1080/17451000.2013.841944.

Rummer, J.L., Munday, P.L., 2017. Climate change and the evolution of reef fishes: past and future. Fish Fish. 18, 22–39. https://doi.org/10.1111/faf.12164.

Ruppert, J.L.W., Vigliola, L., Kulbicki, M., Labrosse, P., Fortin, M.-J., Meekan, M.G., 2018. Human activities as a driver of spatial variation in the trophic structure of fish communities on Pacific coral reefs. Glob. Chang. Biol. 24, e67–e79. https://doi.org/10.1111/gcb.13882.

Russ, G.R., 1987. Is rate of removal of algae by grazers reduced inside territories of

tropical damselfishes? J. Exp. Mar. Biol. Ecol. 110, 1–17. https://doi.org/10.1016/0022-0981(87)90062-1.

Sih, A., Ferrari, M.C.O., Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evol. Appl. 4, 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x.

Simpson, S.D., Radford, A.N., Nedelec, S.L., Ferrari, M.C.O., Chivers, D.P., McCormick, M.I., Meekan, M.G., 2016. Anthropogenic noise increases fish mortality by predation. Nat. Commun. 7, 10544. https://doi.org/10.1038/ncomms10544.

Souza, A.T., Ilarri, M.I., Rosa, I.L., 2011. Habitat use, feeding and territorial behavior of a Brazilian endemic damselfish *Stegastes rocasensis* (Actinopterygii: Pomacentridae). Environ. Biol. Fish 91, 133–144. https://doi.org/10.1007/s10641-010-9765-z.

Titus, B.M., Daly, M., Exton, D.A., 2015. Do reef fish habituate to diver presence? Evidence from two reef sites with contrasting historical levels of SCUBA intensity in the Bay Islands, Honduras. PLoS ONE 10, e0119645. https://doi.org/10.1371/journal.pone.0119645.

Trave, C., Brunnschweiler, J., Sheaves, M., Diedrich, A., Barnett, A., 2017. Are we killing them with kindness? Evaluation of sustainable marine wildlife tourism. Biol. Conserv. 209, 211–222. https://doi.org/10.1016/j.biocon.2017.02.020.

Tuomainen, U., Candolin, U., 2011. Behavioural responses to human-induced environmental change. Biol. Rev. 86, 640–657. https://doi.org/10.1111/j.1469-185X.2010.00164.x.

Watson, D.L., Harvey, E.S., 2007. Behaviour of temperate and sub-tropical reef fishes towards a stationary SCUBA diver. Mar. Freshw. Behav. Physiol. 40, 85–103. https://doi.org/10.1080/10236240701393263.

Wirsing, A.J., Heithaus, M.R., Frid, A., Dill, L.M., 2008. Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. Mar. Mammal. Sci. 24, 1–15. https://doi.org/10.1111/j.1748-7692.2007.00167.x.

Wong, B.B.M., Candolin, U., 2015. Behavioral responses to changing environments. Behav. Ecol. 26, 665–673. https://doi.org/10.1093/beheco/aru183.

Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., McMinds, R., Payet, J.P., Welsh, R., Correa, A.M.S., Lemoine, N.P., Rosales, S., Fuchs, C., Maynard, J.A., Thurber, R.V., 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat. Commun. 7, 11833. https://doi.org/10.1038/ncomms11833.

III. THE DISRUPTIVE INFLUENCE OF HUMAN PRESENCE ON TERRITORIAL BEHAVIOUR OF TWO CORAL REEF DAMSELFISHES

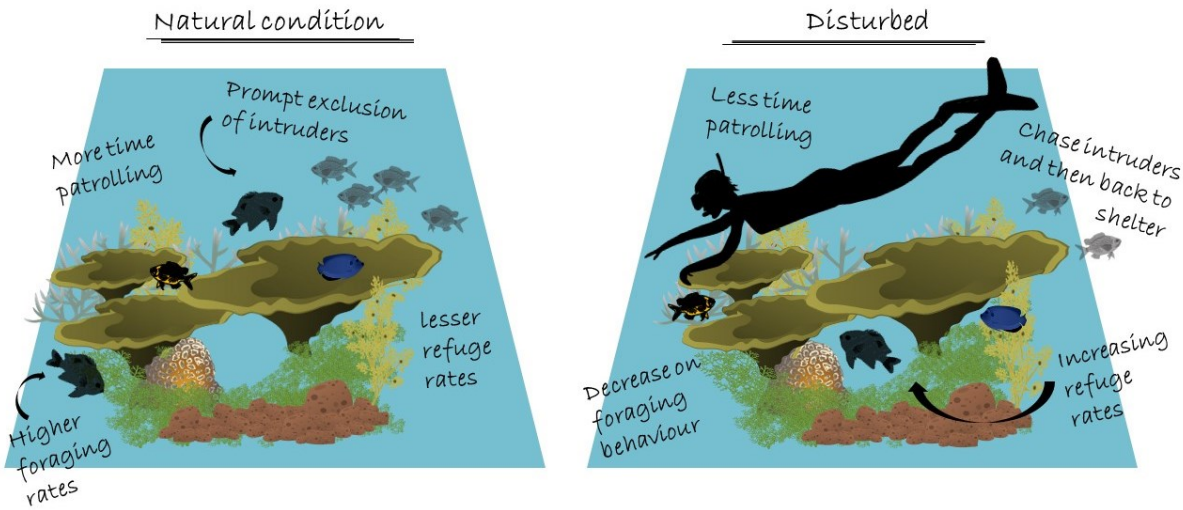
Benevides, L. J [1 *]; Ceccarelli, D.M [2]; Pereira, P. H. C [3]; Cardozo-Ferreira, G.C [4]; Sampaio, C. L. S [1,5]; Jones, G.P [2]

Formatted for Biological Conservation

[1] Programa de Pós-graduação em Diversidade Biológica e Conservação nos Trópicos, Universidade Federal de Alagoas (UFAL), Maceió, Alagoas, Brazil.
[2] Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia
[3] Departamento de Oceanografia, CTG, Universidade Federal de Pernambuco (UFPE), Cidade Universitária, Recife, PE, Brazil.
[4] Laboratório de Ictiologia, Departamento de Oceanografia e Ecologia, Universidade Federal Espírito Santo (UFES), Vitória, Espírito Santo, Brazil.
[5] Laboratório de Ictiologia e Conservação, Universidade Federal de Alagoas (UFAL), Penedo, Alagoas, Brazil.

*benevideslai@gmail.com (corresponding author)

Graphical abstract



Abstract

Human presence is likely to influence the ecology of roving reef fishes by changing their abundance, distribution and wariness, often inducing them to seek shelter or escape. However, how site-attached fish trade-off decisions to keep essential behaviours while dealing with the ongoing human threat in the marine environment is still poorly understood. Here, we tested the relationship between reef fish territorial *vs* risk-taking behaviour under diver presence in *Stegastes apicalis* and *Pomacentrus wardi,* two widespread damselfishes in the northern Great Barrier Reef, east coast of Australia. We hypothesised that damselfishes would spend more time patrolling, defending and foraging in their territories without diver presence. Furthermore, we predicted that larger individuals would spend more time hidden than smaller ones in the diver presence. Overall, both species displayed a similar trend, interrupting their feeding activities to keep temporarily sheltered under diver approach. However, they seemed to maximize food intake when having the opportunity to stay out-of-shelter, even in diver presence. Thus, human presence reduced damselfishes patrolling time, pushing them to search for refuge rather than feeding. Yet, no differences between diver presence *vs* absence or between species were recorded for chasing behaviour. A positive relationship between fish size and refuge behaviour occurred only for *S. apicalis*. The observed shifts on damselfishes essential behaviours would affect their trophic relationships within a community. Monitoring territorial fish behaviour and establishing the consequence of an intermittent human activity on coral reefs is vital to better understand the effects of human presence on reef fish ecology and is valuable for conservation strategies and decision-makers guidance.

Keywords: Non-lethal effects; risk-taking behavior; site-attached fishes; time budget.

Introduction

Anthropogenic influence has been an inevitable and undeniable threat to distinct trophic levels (Bellwood et al., 2019; Dorresteijn et al., 2015). Human encounter can intimidate animals and adaptively increase their stress levels. Eventually, it can lead to deleterious effects (Fowler, 1999; Lima, 1998) or increase energy expenditure, affecting essential functions such as growth and reproduction (Ellenberg et al., 2007; Geffroy et al., 2017). Moreover, human presence might also relax antipredator

behaviour due to repeated interactions with non-threatening visitors (Geffroy et al., 2015). Yet, there is no consensus about such plastic behavioural response. Both prey or predator might increase refuge-seeking behaviour to human activities, where wild animals are chased, stressed and, eventually, harvested (Arlinghaus et al., 2016).

On coral reefs, the detectability of human threat may change accordingly to disturbance level, and thus species can respond differently to diver presence. For example, previous encounters with humans are known to shape reef fish behaviour, increasing and/or modifying wariness along an exploitation gradient of fishing (Januchowski-Hartley et al., 2015), dive gear type and depth (Andradi-Brown et al., 2018). These responses have been drawing the attention of researchers to the potential bias that human effect has on underwater visual censuses (UVCs) results, the most common method for the study of coral reef fishes' abundance and distribution. Studies indicate that fish can be attracted or repelled during diver fish-counting (Dickens et al., 2011; Emslie et al., 2018; Kulbicki et al., 2011; Lopes et al., 2019). Nevertheless, despite fish behavioural changes due to diver presence (Dearden et al., 2010; Pereira et al., 2016) and on presence-absence experimental designs (Benevides et al., 2019; Branconi et al., 2019; Nanninga et al., 2017), knowledge gaps persist on how human presence may disrupt the behaviour of territorial farmer fish that defend territories and the interspecific variations of those effects.

Damselfishes (Pomacentridae) are the most common territorial fishes, defending their habitats from egg-predators and guard their algal farms, on which they cultivate and feed (Bessa and Sabino, 2012; Hata and Kato, 2004). Intensive farmers weed and defend intensively a low diversity of algal turfs, while extensive farmers weed and defend less intensively a diverse algal assemblage (Hata and Kato, 2004). For these fishes, the accurate identification of a threat in reef communities is crucial because the territorial holder encounters individuals from a range of species, and identify which fish pose a great threat allow them to use its energy in the most efficient manner (Schacter et al., 2014). Thereby, if human presence on reefs represents a threat it might bring costs for the damselfish's ability to defend their territories, which may include disruptions on the trade-off between territory patrol time and feeding activities, leading to a decrease in energy intake (Bateman and Fleming, 2017; Lima and Dill, 1990; Schoener, 1987).

In this paper, we tested the impact of snorkeler presence on the behaviour of two common shallow-water damselfish, *Stegastes apicalis* and *Pomacentrus wardi*.

Video cameras deployed were used to quantify fish behaviour in the presence and absence of a snorkeler stimulus. Specifically, we asked: How do damselfish species differ in their territorial behaviour in the presence of snorkelers? We predicted that individuals would spend more time sheltering and would have a decrease in foraging and territorial defence in the presence of divers. We also expected that snorkelers would have a greater impact on the extensive farmers/less aggressive species, *P. wardi*, and on larger individuals.

Material and Methods

Study site and species

We performed our experiment between November 2017 and January 2018 in Arthur Bay (19°7'S, 146°52'E), Magnetic Island National Park, a mainland island located 8km off the coast of North Queensland, Great Barrier Reef, Australia. The national park covers more than half of the island, being mainly surrounded by sandy beaches, coral fringing reefs and mangroves. The sea- and landscape features have been attracting tourists worldwide since the 19th century when it became a popular picnic area (Queensland Goverment, 2018). On Magnetic Island, reef habitats include three main zones: reef flats (dominated by dead corals and fleshy macroalgae); reef crests (high coral cover) and descending reef slope (with coral cover interspersed with patches of macroalgae) (Ceccarelli, 2007).

Two territorial damselfish species (Pomacentridae) were chosen for this study, the intensive farming Australian gregory, *Stegastes apicalis* (De Vis, 1885) and the extensive farming Ward's damsel, *Pomacentrus wardi* Whitley, 1927 (Ceccarelli, 2007; Emslie et al., 2012). Both species defend their territories from grazers, conspecifics and congenerics but differ in territory composition and aggressiveness (Ceccarelli et al., 2005). *Pomacentrus wardi* is usually less energetic when chasing intruders and settle around rocky substrata with relatively high macroalgal abundance, while *S. apicalis* is a harsh defender of their territories, establishing farms on dead coral surfaces on the reef crest (Ceccarelli et al., 2005).

Sampling design and field measurements

Fieldwork was carried out between 9 am and 5 pm, at a maximum depth of 5m. Fish’s total length was visually estimated. Juveniles (i.e. smaller/juvenile-coloured

individuals) and nesting territories were not included in the field observations to avoid ontogenetic and parental care bias, respectively. To record the damselfish behaviour, remote underwater video cameras (GoPro Hero4) were attached to dive weights and deployed on the seafloor at a distance of 1.0 m – 1.5 m from the territories. One video camera was used in each territory to avoid further interference. After deployment, the camera was left to record for 20 min. A fish acclimation period of 3 to 5 min was assumed. Hence, the initial 5 min of each video were excluded from the analysis.

We randomly choose 60 damselfish territories on the Arthur Bay reef. For each species, we selected 30 territories, with 15 treated with a snorkeler stimulus (SS) and 15 representing control territories (CT). Each day, care was taken to maintain a minimum distance of 4 m from one territory to another, preventing disturbance to an individual by the researcher stimulus directed at another individual. For the stimulus treatment, the diver (L.J.B.) swam around the damselfish territory (i.e. swimming above, or at the same depth; approaching the territory and then retreating), simulating the behaviour of a tourist snorkeler (e.g. sometimes looking closer and/or trying to touch the fish). Tourists that approached were directed to stay away, avoiding interference with the behavioural assays.

Statistical methods

All recorded videos were analysed in the Behavioral Observation Research Interactive Software – BORIS (Friard and Gamba, 2016), computing the frequency (number of times/recording minutes) of the following behaviours by each focal individuals: chasing (aggressiveness against other fishes), refuge (hiding in a shelter) and foraging behaviour (bites on the substrate). Furthermore, the time patrolling the territory (proportion of time outside the refuge during the recording minutes) was computed using the same software.

The frequency of damselfishes' behavioural responses between CT *vs* SS were compared using a permutational multivariate analysis of variance (PERMANOVA) with Primer 6+ (Anderson et al., 2008) for each species and between species. It was based on 9999 permutations, a Euclidean resemblance matrix and under the following designs: (a) for comparisons of behaviours between CT *vs* SS for each species, we used 'experimental approach' as a fixed factor with two levels (CT and SS); (b) for each behaviour display compared between species, we used 'experimental approach' and 'species' as a fixed factor with two levels for each one. We used Pearson's correlation

coefficient calculated using ‘corrplot’ package (Wei and Simko, 2017) to investigate relationships among behavioural displays and fish size. Then, we performed a linear regression to illustrate the significant correlations using ‘ggplot2’ package (Wickham, 2016), both in the R environment. A significance level of $\alpha < 0.05$ was considered in the aforementioned analyses.

Results

1. How does the snorkeler presence affect damselfishes’ behaviour?

For both species, patrolling time varied significantly between control (CT) and snorkeler-stimulated (SS) (PERMANOVA – Pseudo-*F* / *p: P. wardi* – 68.18 / *0.00*; *S. apicalis* – 33.65 / *0.00*), with less time spent patrolling around the territory in snorkeler presence (60.6% and 64% of the analysed time for *P. wardi* and *S. apicalis*, respectively) than in snorkeler absence (97.3% and 92%, respectively) (Fig. 1). When patrolling, damselfish usually watch over their territories and display foraging or chasing behaviours, thus the time spent engaging in these activities was expected to be higher in the absence of the snorkeler. However, whilst the aggressive behaviour of both damselfishes did not change with diver presence, feeding activities decreased and the frequency of seeking for refuge increased. Thereby, foraging and refuge rates of *P. wardi* and *S. apicalis* differed between CT and SS territories, but chase rates did not vary significantly (PERMANOVA – Pseudo-*F* / *p*: *P. wardi* - Foraging = 154.62 / *0.00*; Refuge = 9.49 / *0.00;* Chase = 0.67 / *0.44*; *S. apicalis* – Foraging = 5.30 / *0.02*; Refuge = 10.63 / *0.00;* Chase = 0.56 / *0.51*) (Fig. 2).

2. How does the snorkeler presence affect the behaviour between species and among individual sizes?

Chasing behaviour against intruders did not differ between species in diver absence *vs* presence (PERMANOVA – Pseudo-*F* / *p*: Chase = 2.62 / *0.07*). Yet, pair-wise comparisons between species demonstrated differences on refuge behaviour and patrolling time in the absence of a diver (PERMANOVA – Pair-wise: *t* / *p*: Refuge = 4.72 / *0.00*; Patrol time = 3.13 / *0.01*), on which the intensive farmer, *S. apicalis*, used to get inside the refuge more frequently (13.07 n/15min) and spent less time patrolling (13.8 min) than the extensive farmer, *P. wardi* (2.73 n/15min; 14.6 min, respectively)

(Fig. 2). Additionally, foraging rates were higher for *S. apicalis* (33.93 n/15min) than for *P. wardi* (16.4 n/15min) in snorkeler presence (PERMANOVA – Pair-wise: *t* / *p*: Foraging = 2.70 / *0.01*) (Fig. 2).

Correlations among behavioural displays of *P. wardi* in snorkeler absence have shown that chasing behaviour increased with increasing refuge rates and, as expected, refuge rates decreased according to increasing in patrol time. In turn, when in snorkeler presence, an increase in patrol time also increased the frequency of chasing behaviour against intruders (Fig. 3; Fig. 1S). Similar to *P. wardi*, the refuge rates of *S. apicalis* in snorkeler absence also had a negative correlation with patrol time. However, in diver presence, *S. apicalis* increased the foraging rates as increased the frequency of refuge (Fig. 3; Fig. 1S). The relationship among behavioural displays and fish size was only observed for *S. apicalis*, where larger individuals refuged more frequently than the smaller ones in diver presence (Fig. 3; Fig. 1S).

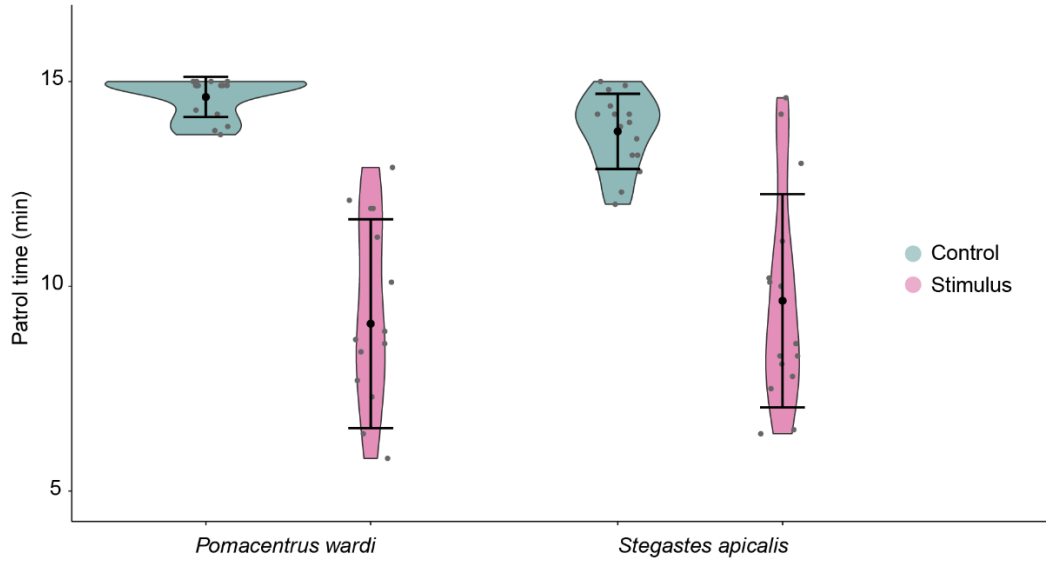


Figure 1. Patrol time comparisons between the absence *vs* presence of snorkeler (control *vs* stimulus, respectively) for each species: *Pomacentrus wardi* and *Stegastes apicalis*. Beans represent the density of the points. Grey points are the raw data, larger black points represent the mean values and error bars are a standard deviation.

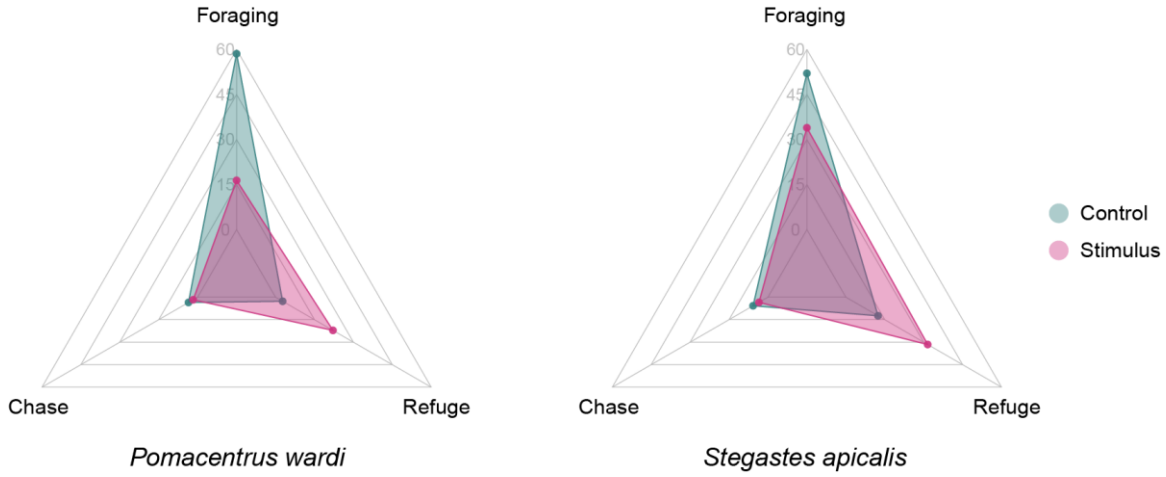


Figure 2. Frequency (N/15min – medians of the triangle) of behavioural displays of damselfishes' while in the absence *vs* presence (control vs stimulus) of snorkeler around the territory of each species, *Pomacentrus wardi* (left) and *Stegastes apicalis* (right). Dots represent the average frequency of each behaviour in each experimental approach.

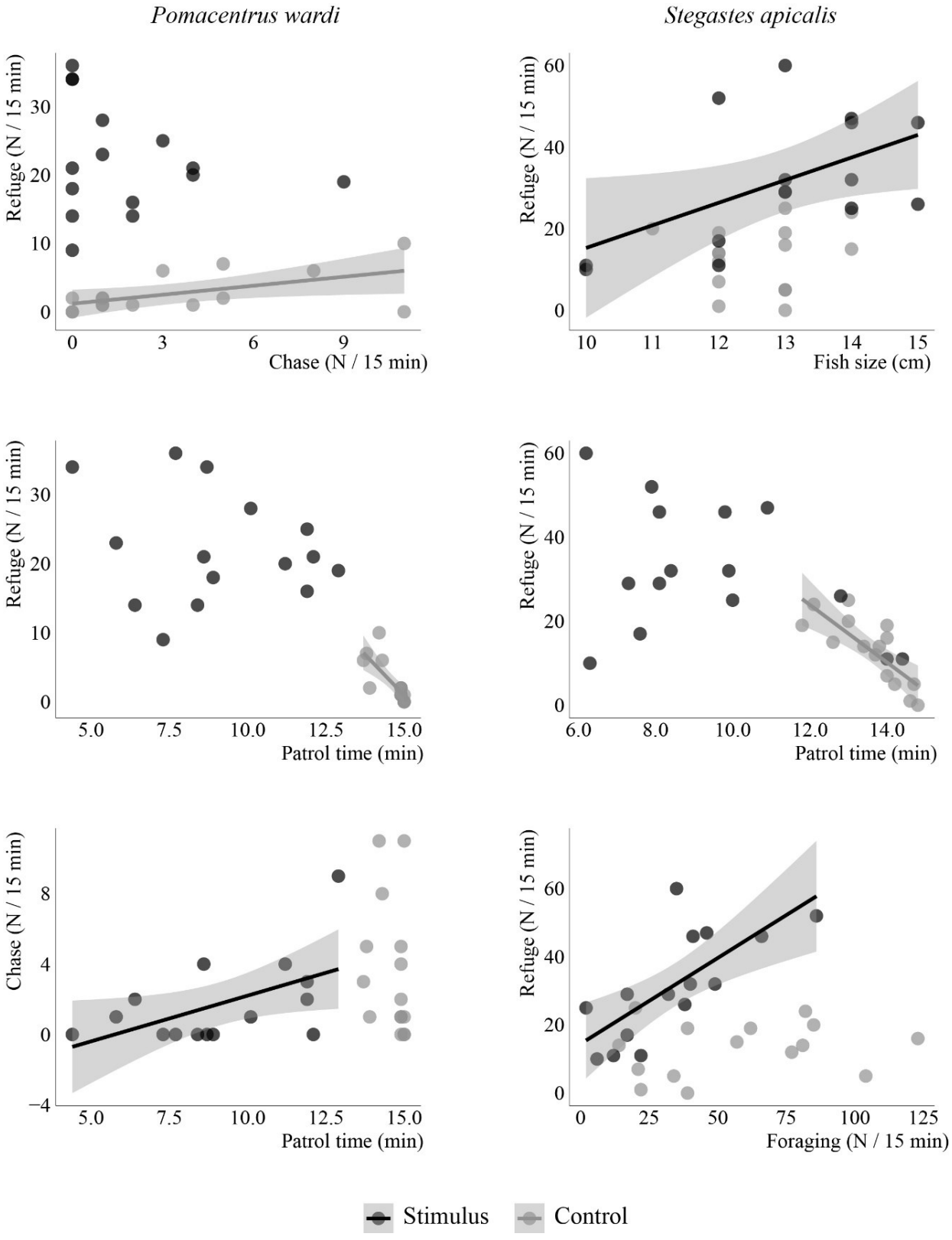


Figure 3. Linear regressions among behavioural displays of *Pomacentrus wardi* (left) and *Stegastes apicalis* (right) in diver absence (control/light grey dots) and during snorkeler approach (stimulus/dark grey dots). Significant results are indicated by trend line. For all comparisons and R values, check supplemental material.

Discussion

Similar to natural predators, humans usually visit reef systems in variable ways, with temporal changes depending on diurnal (e.g. morning, afternoon, or night) or seasonal cycles (e.g. summer seasons), and can push animals to adjust their behaviour to adaptatively balance fitness-enhancing activities and predation risk (Blumstein et al., 2017). However, different fish species can exhibit different responses to human's fear-effect in marine systems. This study investigated the humans' presence over the behaviour of two territorial damselfishes in a tourist-visited reef at the Great Barrier Reef. Overall, diver approach elevated the damselfishes' wariness above the benefits of remaining exposed, pushing them to seek refuge rather than continue to engage in foraging behaviour. As predicted, damselfishes spent less time patrolling their territories under snorkeler disturbance. Yet, no significance was recorded between chasing rates against intruders on snorkeler presence *vs* absence. Our results indicate that threat effects of humans' presence can impair essential activities of both *Stegastes apicalis* and *Pomacentrus wardi*.

In diver presence, damselfishes were observed leaving the shelter, chasing intruders away and quickly returning into the refuge. Possibly, this behaviour has balanced the agonistics interactions between the territory-holder and intruders, with or without the disturbance of a diver. However, it has delayed the prompt exclusion of competitor herbivorous fish after invasion. This delay would allow invaders to take advantage of an undefended spot of food source and alter the algal biomass inside damselfish territories (Hata and Kato, 2004). Although changes on foraging patterns of roving herbivorous through agonistic behaviour by farmer fishes may not be applicable for all species (Eurich et al., 2018), this changes can shape the benthic assemblage and thus it is an essential functional process to the reef community (Ceccarelli, 2007). On the other hand, damselfish aggression is not the primary mechanism by which benthic assemblages are controlled by the territory holder. Farmer species play a central role in determining the structure of algal communities by actively cultivating a unique set of algae to fit their resource requirements (Ceccarelli et al., 2011).

Specialists such as damselfishes have also an ecologically important role as benthic feeders (Ceccarelli, 2007; Ceccarelli et al., 2001). Their fast mouth closing mechanism and accurate bites enable them to be highly selective, eating tiny filamentous algae and weeding unwanted or unpalatable algae (Ceccarelli, 2007;

Olivier et al., 2016). Yet, the observed decrease on the foraging behaviour of *S. apicalis* and *P. wardi* is likely to affect either the individual fitness, due reduction in energy intake, as well as their trophic relationships within a community. For instance, *S. apicalis* can decelerate the succession at an early stage dominated by filamentous algae, altering the successional pathways and benthic communities within their territories but also promoting grown of algal communities visually and taxonomically distinct from surrounding areas (Ceccarelli et al. 2011). Therefore, if fish interrupt foraging activity to refuge from the closest approach of a snorkeler, we would expect shifts on the algal grown trajectories and species interactions inside and outside damselfish territories. Here we were unable to perform long-term observations of damselfish behaviour and compare the potential for indirect consequences of human presence on trophic dynamics. Further investigation must include long-term differences on composition before-after disturbances of snorkelers on damselfish behaviour.

Unexpectedly, damselfishes seem to trade-off the wasted time sheltered by enhancing feeding intake when out-of-shelter. Even when snorkeler was swimming around, the foraging rates of *S. apicalis* had proportionally increased according to refuge frequency. Furthermore, larger individuals of *S. apicalis* sought refuge more frequently than smaller ones under the snorkeler approach. This trend might be resulting from the higher metabolic requirements of smaller individuals (Meuthen et al., 2019), which forces them to behave boldly and foraging outside the refuge more frequently than larger fish. This behavioural plasticity may provide a potential advantage to the organism's life, shaping the ability of young individuals to interact with predators, conspecifics and the complex 3-dimensional maze of reef environments (Meuthen et al., 2019). Another explanation is related to the experiences of fishes exposed to a variety of threats at distinct stages of their development. Ontogenetic changes on antipredator behaviour are usually reported associated with experiences of being a targeted species in human predatory activities, where larger fish are more alert, escaping or refuging from spear-fishers approaching (Gotanda et al., 2009; Januchowski-Hartley et al., 2015; Nunes et al., 2018), albeit size-related escape behaviours may not be a rule for reef fishes (Benevides et al., 2018). Similarly, learning through experiences not related to predator attack may also provide an opportunity for larger fish exhibit avoidances responses (Kelley and Magurran, 2003).

Despite the impacts of human activities on the marine environment keep advancing (e.g. pollution, fishing, climate change), popularization of the recreational diving industry remains to arise and these combined impacts may compromise species resilience (Giglio et al., 2020; Hughes et al., 2017). Even though most recreational divers do not have the intention to kill or catch, the unpredictability of encounters or attack rates by humans makes our presence costly and a potential threat for reef fish. Indeed, being flexible to an unpredictable risky encounter can be costly and drive animals to waste energy with unnecessary antipredator behaviour or to lose opportunities to increase energy intake (Thomson et al., 2012). In accordance, we have shown that different damselfish species similarly avoid a human harmless approach, temporarily losing potential chances to retain food intake and kept sheltered as long as necessary. While the snorkeler looked for it or simply swam around the damselfish territories, individuals have hidden and decreased about 30% of their time from patrolling to retreating.

On reefs frequently used for ecotourism, humans chase fish and cause behavioural disruptions with cameras (De Brauwer et al., 2019; Giglio et al., 2018) when trying to get closely images. They also produce noise with SCUBA apparatus (Lobel, 2005; Lopes et al., 2019) and motorboats (Simpson et al., 2016). Humans behave oddly and carelessly touch reef structures and organisms when struggling with dive buoyancy (Giglio et al., 2016), beyond disturb reef fish essential activities (Di Franco et al., 2013; Titus et al., 2015). Therefore, human presence usually elicits antipredator responses and behavioural disruptions similar to those observed when animals face a predator, even in the absence of a lethal effect (Gaynor et al., 2019). However, it is still uncertain if the cumulative impacts of repeated human visitations on reef systems can either lead to chronic stress on individual fitness, or to a reduction in stress response over time.

For a better understanding about the trade-off decisions of territorial fishes under human presence, it is also important to couple behavioural outcomes with an inherent physiological response and body condition when individuals are disturbed in visited and non-visited areas. In the long-term, monitoring effort on territorial fish behaviour would be able to identify less disruptive diving practices for maintenance of the ecological role of damselfish on coral reefs. It would also provide major insights into species' ability to respond to the current and emerging disturbances, and how they can persist on frequently impacted reefs.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Acknowledgements

We would like to thank J. Howard Choat, Maya Srinivasan, and Jones's lab students for all kindness and guidance. We also thank the support provide by the ARC Centre of Excellence for Coral Reef Studies, James Cook University, Australia. L.J.B was supported by CAPES, Higher Education Personnel Improvement Coordination – Brazil. GCCF was supported by FAPES, Foundation for research support of Espírito Santo State – Brazil.

References

Anderson, M., Gorley, R.N., Clarke, R.K., 2008. PERMANOVA + for PRIMER: Guide to software and statistical methods, PRIMER-E. Plymouth, UK.

Andradi-Brown, D.A., Gress, E., Laverick, J.H., Monfared, M.A.A., Rogers, A.D., Exton, D.A., 2018. Wariness of reef fish to passive diver presence with varying dive gear type across a coral reef depth gradient. J Mar Biol Assoc United Kingdom 98, 1733–1743. doi:10.1017/S0025315417001278

Arlinghaus, R., Alós, J., Klefoth, T., Laskowski, K., Monk, C.T., Nakayama, S., Schröder, A., 2016. Consumptive tourism causes timidity, rather than boldness, Syndromes: a response to Geffroy et al. Trends Ecol Evol 31, 92–94. doi:10.1016/j.tree.2015.11.008

Barker, N.H.L., Roberts, C.M., 2004. Scuba diver behaviour and the management of diving impacts on coral reefs. Biol Conserv 120, 481–489. doi:10.1016/j.biocon.2004.03.021

Bateman, P.W., Fleming, P.A., 2017. Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. Biol Conserv 211, 10–19. doi:10.1016/j.biocon.2017.05.003

Bellwood, D.R., Pratchett, M.S., Morrison, T.H., Gurney, G.G., Hughes, T.P., Álvarez-Romero, J.G., Day, J.C., Grantham, R., Grech, A., Hoey, A.S., Jones, G.P., Pandolfi, J.M., Tebbett, S.B., Techera, E., Weeks, R., Cumming, G.S., 2019. Coral reef conservation in the Anthropocene: Confronting spatial mismatches

and prioritizing functions. Biol Conserv 236, 604–615. doi:10.1016/j.biocon.2019.05.056

Benevides, L.J., Cardozo-Ferreira, G.C., Ferreira, C.E.L., Pereira, P.H.C., Pinto, T.K., Sampaio, C.L.S., 2019. Fear-induced behavioural modifications in damselfishes can be diver-triggered. J Exp Mar Bio Ecol 514–515, 34–40. doi:10.1016/j.jembe.2019.03.009

Benevides, L.J., Pinto, T.K., Nunes, J. de A.C.C., Sampaio, C.L.S., 2018. Fish escape behavior as a monitoring tool in the largest Brazilian multiple-use Marine Protected Area. Ocean Coast Manag 152, 154–162. doi:10.1016/j.ocecoaman.2017.11.029

Bessa, E., Sabino, J., 2012. Territorial hypothesis predicts the trade off between reproductive opportunities and parental care in three species of damselfishes (Pomacentridae: Actinopterygii). Lat Am J Aquat Res 40, 134–141. doi:10.3856/vol40-issue1-fulltext-13

Branconi, R., Wong, M.Y.L., Buston, P.M., 2019. Comparison of efficiency of direct observations by scuba diver and indirect observations via video camera for measuring reef-fish behaviour. J Fish Biol jfb.13921. doi:10.1111/jfb.13921

Ceccarelli, D.M., 2007. Modification of benthic communities by territorial damselfish: a multi-species comparison. Coral Reefs 26, 853–866. doi:10.1007/s00338-007-0275-1

Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2011. Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. J Exp Mar Bio Ecol 399, 60–67. doi:10.1016/j.jembe.2011.01.019

Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2005. Effects of territorial damselfish on an algal-dominated coastal coral reef. Coral Reefs 24, 606–620. doi:10.1007/s00338-005-0035-z

De Brauwer, M., Gordon, L.M., Shalders, T.C., Saunders, B.J., Archer, M., Harvey, E.S., Collin, S.P., Partridge, J.C., McIlwain, J.L., 2019. Behavioural and pathomorphological impacts of flash photography on benthic fishes. Sci Rep 9, 748. doi:10.1038/s41598-018-37356-2

Dearden, P., Theberge, M., Yasué, M., 2010. Using underwater cameras to assess the effects of snorkeler and SCUBA diver presence on coral reef fish abundance, family richness, and species composition. Environ Monit Assess 163, 531–538. doi:10.1007/s10661-009-0855-3

Di Franco, A., Baiata, P., Milazzo, M., 2013. Effects of recreational scuba diving on mediterranean fishes: Evidence of involuntary feeding? Mediterr Mar Sci 14, 15–18. doi:10.12681/mms.321

Dickens, L.C., Goatley, C.H.R., Tanner, J.K., Bellwood, D.R., 2011. Quantifying relative diver effects in underwater visual censuses. PLoS One 6, e18965. doi:10.1371/journal.pone.0018965

Dorresteijn, I., Schultner, J., Nimmo, D.G., Fischer, J., Hanspach, J., Kuemmerle, T., Kehoe, L., Ritchie, E.G., 2015. Incorporating anthropogenic effects into trophic ecology: predator–prey interactions in a human-dominated landscape. Proc R Soc B Biol Sci 282, 20151602. doi:10.1098/rspb.2015.1602

Ellenberg, U., Setiawan, A.N., Cree, A., Houston, D.M., Seddon, P.J., 2007. Elevated hormonal stress response and reduced reproductive output in Yellow-eyed penguins exposed to unregulated tourism. Gen Comp Endocrinol 152, 54–63. doi:10.1016/j.ygcen.2007.02.022

Emslie, M.J., Cheal, A.J., MacNeil, M.A., Miller, I.R., Sweatman, H.P.A., 2018. Reef fish communities are spooked by scuba surveys and may take hours to recover. PeerJ 6, e4886. doi:10.7717/peerj.4886

Emslie, M.J., Logan, M., Ceccarelli, D.M., Cheal, A.J., Hoey, A.S., Miller, I., Sweatman, H.P.A., 2012. Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. Mar Biol 159, 1293–1304. doi:10.1007/s00227-012-1910-0

Eurich, J.G., Shomaker, S.M., McCormick, M.I., Jones, G.P., 2018. Experimental evaluation of the effect of a territorial damselfish on foraging behaviour of roving herbivores on coral reefs. J Exp Mar Bio Ecol 506, 155–162. doi:10.1016/J.JEMBE.2018.06.009

Fowler, G.S., 1999. Behavioral and hormonal-responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. Biol Conserv 90, 143–149. doi:10.1016/S0006-3207(99)00026-9

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol Evol 7, 1325–1330. doi:10.1111/2041-210X.12584

Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E., Brashares, J.S., 2019. Landscapes of Fear: spatial patterns of risk perception and response. Trends Ecol Evol 34, 355–368. doi:10.1016/j.tree.2019.01.004

Geffroy, B., Samia, D.S.M., Bessa, E., Blumstein, D.T., 2015. How nature-based tourism might increase prey vulnerability to predators. Trends Ecol Evol 30, 755–765. doi:10.1016/j.tree.2015.09.010

Geffroy, Benjamin;, Sadoul, B., Ellenberg, U., 2017. Physiological and behavioral consequences of human visitation, in: Blumstein, D.T., Geffroy, Benjamin, Samia, D.S.M., Bessa, E. (Eds.), Ecotourism's Promise and Peril. Springer International Publishing, Cham, pp. 9–27. doi:10.1007/978-3-319-58331-0_2

Giglio, V.J., Luiz, O.J., Ferreira, C.E.L., 2020. Ecological impacts and management strategies for recreational diving : A review. J Environ Manage 256, 109949. doi:10.1016/j.jenvman.2019.109949

Giglio, V.J., Luiz, O.J., Schiavetti, A., 2016. Recreational diver behavior and contacts with benthic organisms in the Abrolhos national marine park, Brazil. Environ Manage 57, 637–648. doi:10.1007/s00267-015-0628-4

Giglio, V.J., Ternes, M.L.F., Kassuga, A.D., Carlos, E.L., 2018. Scuba diving and sedentary fish watching : effects of photographer approach on seahorse behavior. J Ecotourism 0, 1–10. doi:10.1080/14724049.2018.1490302

Gotanda, K.M., Turgeon, K., Kramer, D.L., 2009. Body size and reserve protection affect flight initiation distance in parrotfishes. Behav Ecol Sociobiol 63, 1563–1572. doi:10.1007/s00265-009-0750-5

Hata, H., Kato, M., 2004. Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. J Exp Mar Bio Ecol 313, 285–296. doi:10.1016/j.jembe.2004.08.009

Hawkins, J.P., Roberts, C.M., Van'T Hof, T., De Meyer, K., Tratalos, J., Aldam, C., 1999. Effects of recreational scuba diving on caribbean coral and fish communities. Conserv Biol 13, 888–897. doi:10.1046/j.1523-1739.1999.97447.x

Januchowski-Hartley, F.A., Graham, N.A.J., Cinner, J.E., Russ, G.R., 2015. Local fishing influences coral reef fish behavior inside protected areas of the Indo-Pacific. Biol Conserv 182, 8–12. doi:10.1016/j.biocon.2014.11.024

Kelley, J.L., Magurran, A.E., 2003. Learned predator recognition and antipredator responses in fishes. Fish Fish 4, 216–226. doi:10.1046/j.1467-2979.2003.00126.x

Kulbicki, Y.B.M., Laloe, F., Bozec, Y.-M., Kulbicki, M., Laloë, F., Mou-Tham, G., Gascuel, D., 2011. Factors affecting the detection distances of reef fish: implications for visual counts. Mar Biol 158, 969–981. doi:10.1007/s00227-011-

1623-9

Lima, S.L., 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives, in: Advances in the Study of Behavior. pp. 215–290. doi:10.1016/S0065-3454(08)60366-6

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68, 619–640. doi:10.1139/z90-092

Lobel, P.S., 2005. Scuba bubble noise and fish behavior: a rationale for silent diving technology. Diving Sci Proc Am Acad Underw Sci 49–59.

Lopes, K.H., Williams, I.D., Kosaki, R.K., Gray, A.E., Leonard, J.C., 2019. Effects of SCUBA bubbles on counts of roving piscivores in a large remote marine protected area. PLoS One 14, e0226370. doi:10.1371/journal.pone.0226370

Meuthen, D., Ferrari, M.C.O., Lane, T., Chivers, D.P., 2019. Plasticity of boldness: high perceived risk eliminates a relationship between boldness and body size in fathead minnows. Anim Behav 147, 25–32. doi:10.1016/j.anbehav.2018.11.003

Nanninga, G.B., Côté, I.M., Beldade, R., Mills, S.C., 2017. Behavioural acclimation to cameras and observers in coral reef fishes. Ethology 123, 705–711. doi:10.1111/eth.12642

Nunes, J.A.C.C., Costa, Y., Blumstein, D.T., Leduc, A.O.H.C., Dorea, A.C., Benevides, L.J., Sampaio, C.L.S., Barros, F., 2018. Global trends on reef fishes' ecology of fear: Flight initiation distance for conservation. Mar Environ Res 136, 153–157. doi:10.1016/j.marenvres.2018.02.011

Olivier, D., Frederich, B., Parmentier, E., 2016. Cerato-mandibular ligament: a key trait in damselfishes?, in: Bruno Frédérich, E.P. (Ed.), Biology of Damselfishes. CRC Press, Taylor & Francis, p. 340.

Pereira, P.H.C., Leal, I.C.S., de Araújo, M.E., 2016. Observer presence may alter the behaviour of reef fishes associated with coral colonies. Mar Ecol 37, 760–769. doi:10.1111/maec.12345

Queensland Goverment, 2018. Magnetic Island National Park [WWW Document]. Dep Environ Sci. URL https://parks.des.qld.gov.au/parks/magnetic-island/about.html (accessed 3.3.18).

Schacter, C.R., Albright, L.B., Dubofsky, E.A., Fitzsimmons, J.N., Focht, R., Nadler, L.E., Sandercock, M., Taylor, L., Walfoort, D., Whitten, T., Williams, L.J., Rosenthal, G.G., 2014. Risk-sensitive resource defense in a territorial reef fish.

Environ Biol Fishes 97, 813–819. doi:10.1007/s10641-013-0181-z

Schoener, T.W., 1987. Time budgets and territory size: some simultaneous optimization models for energy maximizers. Am Zool 27, 259–291. doi:10.1093/icb/27.2.259

Simpson, S.D., Radford, A.N., Nedelec, S.L., Ferrari, M.C.O., Chivers, D.P., McCormick, M.I., Meekan, M.G., 2016. Anthropogenic noise increases fish mortality by predation. Nat Commun 7, 10544. doi:10.1038/ncomms10544

Titus, B.M., Daly, M., Exton, D.A., 2015. Do reef fish habituate to diver presence? evidence from two reef sites with contrasting historical levels of SCUBA intensity in the Bay islands, Honduras. PLoS One 10, e0119645. doi:10.1371/journal.pone.0119645

Wei, T., Simko, V., 2017. Package “corrplot”: Visualization of a correlation matrix (Version 0.84). https://github.com/taiyun/corrplot.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis.

Supplementary material

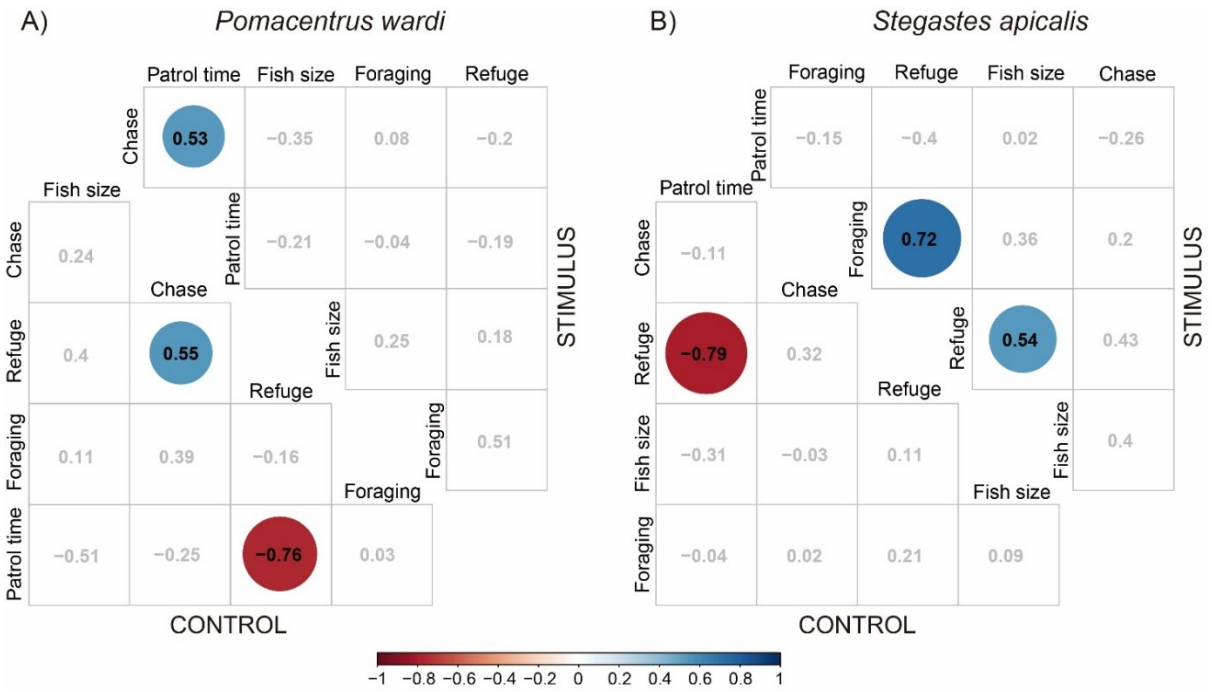


Figure S1: Pearson's correlations among the fish size and behavioural displays (foraging, chasing and refuge rates and patrol time) between the experimental approaches (control *vs* stimulus) for each species: A) *Pomacentrus wardi*; B) *Stegastes apicalis*. Coloured circles represent significant correlations. Numbers inside the coloured circles represent R-values.

IV. HUMAN INTIMIDATION ON REEFS IMPAIRS FORAGING RATES OF TERRITORIAL FISHES

Benevides, L. J [1 *]; Pereira, P. H. C [2,] Sampaio, C. L. S [1,3]

Formatted for Coral Reefs 'Notes'

[1] Programa de Pós-graduação em Diversidade Biológica e Conservação nos Trópicos, Universidade Federal de Alagoas (UFAL), Maceió, Alagoas, Brazil.
[2] Departamento de Oceanografia, CTG, Universidade Federal de Pernambuco (UFPE), Cidade Universitária, Recife, PE, Brazil.
[3] Laboratório de Ictiologia e Conservação, Universidade Federal de Alagoas (UFAL), Penedo, Alagoas, Brazil.

*benevideslai@gmail.com (corresponding author)

Abstract

Territorial reef fishes can adjust their behaviours to deal with predation, however, the costs of human non-predatory disturbance for these fish might have been underestimated. Herein, we examined a damselfish' risk-perception to a disturbance posed by a predator model and diver presence. Complementarily, we gathered foraging shifts under diver encounter of four damselfishes from three distinct reef systems. At a remote reef, no differences in aggressiveness or sheltering responses were recorded but *Stegastes sanctipauli* reduced approximately three times the foraging activity in response to diver and about twice in predator model presence. Besides, *S. sanctipauli* did not effectively distinguished both threat-stimuli, suggesting a wide generalization of predator recognition. The other three species living in touristic areas in the Atlantic and Pacific oceans have also decreased their foraging to diver presence. Human intimidation in reefs impair damselfishes' food exploration and it would affect fish fitness and community dynamics in pristine and recreational areas.

Keywords: Damselfishes; diver-disturbance; food intake; non-consumptive effects; predator model.

Introduction

For centuries humans have been transiting between terrestrial and marine environments, exploring all resources needed or wanted. With our particularly intense exploitation and unique predatory behaviour, we have become a 'super-predator' that

continually alters ecological and evolutionary processes of terrestrial and marine populations (Darimont et al. 2015). If you are not a hunter or a fisher, you might be thinking that you do not fit in the above statement, but you do. That is why some animals run away when we try to approach them, even having no intention to hurt them. Growing evidence suggests that non-lethal human disturbance also have the potential to create a landscape of fear by increasing the animal's investment in antipredator behaviours, as wariness and flight (Januchowski-Hartley et al. 2011; Madin et al. 2016).

In marine systems, while is known that fish can adaptatively learn to adjust its behaviours to deal with disturbances from predatory human activities (i.e. fishing) (Januchowski-Hartley et al. 2011), the non-consumptive effects (NCEs) of recreational activities (e.g. Scuba or free diving) on fishes remain underestimated (but see Huddart and Stott 2019; Matassa et al. 2016). Alike other animals, for territorial fishes, the costs of responding to a non-predatory disturbance (i.e. running away or hiding) could be as high as those responses to a predatory one. Territorial fishes dedicate most of their time patrolling their territory, excluding intruders or guarding their eggs, which are highly energic activities and are often associated with foraging and/or mating (Cleveland 1999; Kaufmann 1983). Damselfishes (Pomacentridae), beyond tough territorial defenders, are also known to maintain a remarkable algal farming, strongly influencing the benthic communities and fish dynamics on coral reefs (Jones et al. 2006). Therefore, any level of disturbance posed by humans represents an additional threat either for the territorial holder, which must be able to balance between take the risk or efficiently defend its resources (in terms of food intake) or for the marine species dynamics.

Since human disturbance (e.g. fishing, recreational activities) globally continues advancing faster than natural perturbations (e.g. oceanographic events such as El Niño Southern Oscillation), understand how site-attached fish species recognize and respond towards diver presence would provide a broad perspective about our risk-effects in a human-dominated seascape. Here, we examined whether the damselfish *Stegastes sanctipauli* Lubbock & Edwards, 1981 distinguish their risk-perception (i.e. changes in chase, refuge and foraging behaviours) to a predator model of the great barracuda, *Sphyraena barracuda* Walbaum, 1792, and diver approach at St Paul's Rocks, the smallest and remote archipelago in Equatorial Atlantic. Complementarily, to a broad-view of damselfishes behavioural patterns to humans' NCEs, we gathered foraging shifts under diver encounter of four damselfish species, *Stegastes sanctipauli,*

Stegastes fuscus, Stegastes apicalis and *Pomacentrus wardi,* from three distinct reef systems on Brazil and Australia: remote island reef, recreational coastal reef and recreational mainland island reef.

Material and Methods

Data for *S. fuscus* (n = 30), *S. apicalis* (n = 30) and *P. wardi* (n = 30) were reanalysed from Benevides et al. (2019) and Chapter 2. Study on *S. fuscus* was conducted at the Arraial do Cabo Marine Extractive Reserve, Southeastern Brazil, a recreational coastal rocky reef in a high-tourist-visited inlet (23° 4' 7"S; 41° 57' 49"W), and for *S. apicalis* and *P. wardi* at the Magnetic Island (19° 7' 44"S; 146° 52' 38"E), a recreational island reef in Great Barrier Reef, Northeast Australia. More details on sites description and methods applied on behavioural assays, see Benevides et al. (2019) and Chapter 2. Data from these species were gathered to those from *Stegastes sanctipauli*, the endemic territorial damselfish from Saint Peter and Saint Paul Archipelago (SPSPA). SPSPA is an insular group of five remote islets located in the Mid-Atlantic Ridge, about 1000 km off the northeastern Brazilian coast. It presents the highest local reef fish endemism (9%) in the southwestern Atlantic (Pinheiro et al. 2018). Our sampling was carried out at the small inlet in SPSPA, where the reef zone has a horizontal slope of 30m followed by an abrupt vertical wall (Magalhães et al. 2015).

To record the *S. sanctipauli* behaviour during each disturbance treatment and control, a remote underwater video camera (GoPro Hero4) was attached to dive weights and deployed on the seafloor at a distance of 1.0 m – 1.5 m from the territories. After deployed, the camera was left recording for 15 min. A fish acclimation period between 3 to 5 min was assumed. Hence, the initial 5 min of each video were excluded from the analysis. Juveniles and nesting territories were not included in the field observations. For the ‘human disturbance treatment’ (HDT), a SCUBA diver (L.J.B.) swam around the damselfish territory. For the ‘predator disturbance treatment’ (PDT) we used a fibreglass model of the *Sphyraena barracuda* (ca. 80-cm total length), which was deployed on the seafloor near the damselfish territories within the camera viewing angle (Fig. 1B, C). We randomly picked 35 damselfish territories, with 11 being treated as HDT, 11 treated as PDT and 13 representing control territories (CT). We maintained a minimum distance of 4 m from one territory to another, preventing disturbance by the

researcher stimulus at another individual. Each assay was performed between 9 am and 2 pm at an average depth of 8.2 m.

We analysed videos in the Behavioral Observation Research Interactive Software – BORIS (Friard and Gamba 2016), computing the frequency (number of times/recording minutes) of chasing (aggressiveness against other fishes), refuge (hiding in a shelter) and foraging behaviour (bites on the substrate) displayed by *S. sanctipauli*. We also computed the hiding time (proportion of time inside the refuge during the recording minutes) using the same software. Damselfish's behavioural frequencies were compared using a permutational multivariate analysis of variance (PERMANOVA) and pair-wise tests with Primer 6+ (Anderson, Gorley, and Clarke 2008). For *S. sanctipauli,* we compared between each disturbance assays (HDT and PDT) and control following the design: (i) 'disturbance treatment' as a fixed factor with three levels (HDT, PDT and control). Besides, we compared foraging displays of each studied species during HDT to control as following: 'disturbance treatment' as a fixed factor with two levels (HDT and control), and 'species' as a fixed factor with four levels (*S. sanctipauli*, *S. fuscus, S. apicalis* and *P. wardi*). It was based on 9999 permutations and a Euclidean resemblance matrix. A significance level of $\alpha < 0.05$ was considered in all analyses.

Results and Discussion

Our results revealed no significant differences in aggressiveness or sheltering responses from territorial fishes that received disturbance posed by a predator model and diver presence in ASPSP. However, *S. sanctipauli* reduced the foraging activity in response to both treatments compared to control. Foraging rates of *S. sanctipauli* differed between control *vs* diver presence (PERMANOVA – Pseudo-t: 4.08/ *p: 0.00*), and control *vs* barracuda model (PERMANOVA – Pseudo-t: 2.59/ *p: 0.01*), reducing approximately three times with the diver approach (20.3 bites/ 10 min) (Fig. 2A) and about twice in predator model presence (32.1 bites/ 10 min) compared to control (52.5 bites/ 10 min). A similar suppression in feeding activities caused by predator model has been previously verified in parrotfish and surgeonfish in the Florida Keys reef, suggesting that this transitory predator may generate a 'zone of fear' with different temporal and spatial scales (Catano et al. 2017). This foraging suppression indicates that damselfish have been vigilant to human and barracuda model presence and that

these threats are likely to reduce their feeding activity with long-term fitness consequences.

Considering that no recreational diving activity is allowed at SPSPA and the presence of researcher divers is sporadic, we expected to record a non-significant human presence effect rather than an increase in the threat-sensitive perception of *S. sanctipauli*. Following this prediction, a recent study indicates that the site isolation and absence of spearfishing have reduced the wariness of five reef species living in that oceanic island compared to studies in human-dominated coastal reef systems (Nunes et al. 2019). Nevertheless, even transitory, the researcher dive activities as well as the recreational fisheries, conducted mainly when the research station is occupied by Brazilian Navy personnel (Giglio et al. 2018), appear to stress and make fish react according to the risk-perception learning. Thus, these fish could be using memory abilities to recognize humans as a predator (Darimont et al. 2015; Kelley and Magurran 2003; Triki and Bshary 2019), and despite not being a target, damselfish seems to prefer not to take the risk of allowing human approach without being vigilant.

On the other hand, comparisons between diver and a barracuda model disturbances have shown no significant differences in chasing behaviour (PERMANOVA – Pseudo-t: 0.52 / *p: 0.62*), refuge rates (PERMANOVA – Pseudo-t: 1.40/ *p: 0.19*), hiding time (PERMANOVA – Pseudo-t: 1.38 / *p: 0.12*) or foraging rates of *S. sanctipauli* (PERMANOVA – Pseudo-t: 1.98 / *p: 0.06*). This equivalent behavioural outcome suggests that *S. sanctipauli* have a wide generalization window of predator recognition, do not effectively distinguish both threat-stimuli and maintaining similar patterns of food resource use, vigilance and active defence (Fig. 1). Overall, the damselfish's predator recognition appears to be shaped by a momentary assessment of the likelihood of an attack (i.e. in presence of diver or predator model), usually exposing individuals to a risk paradox between being more vigilant or forage more in high- and low-risk periods (Benevides et al. 2019; Ferrari, Sih, and Chivers 2009; Chapter 2).

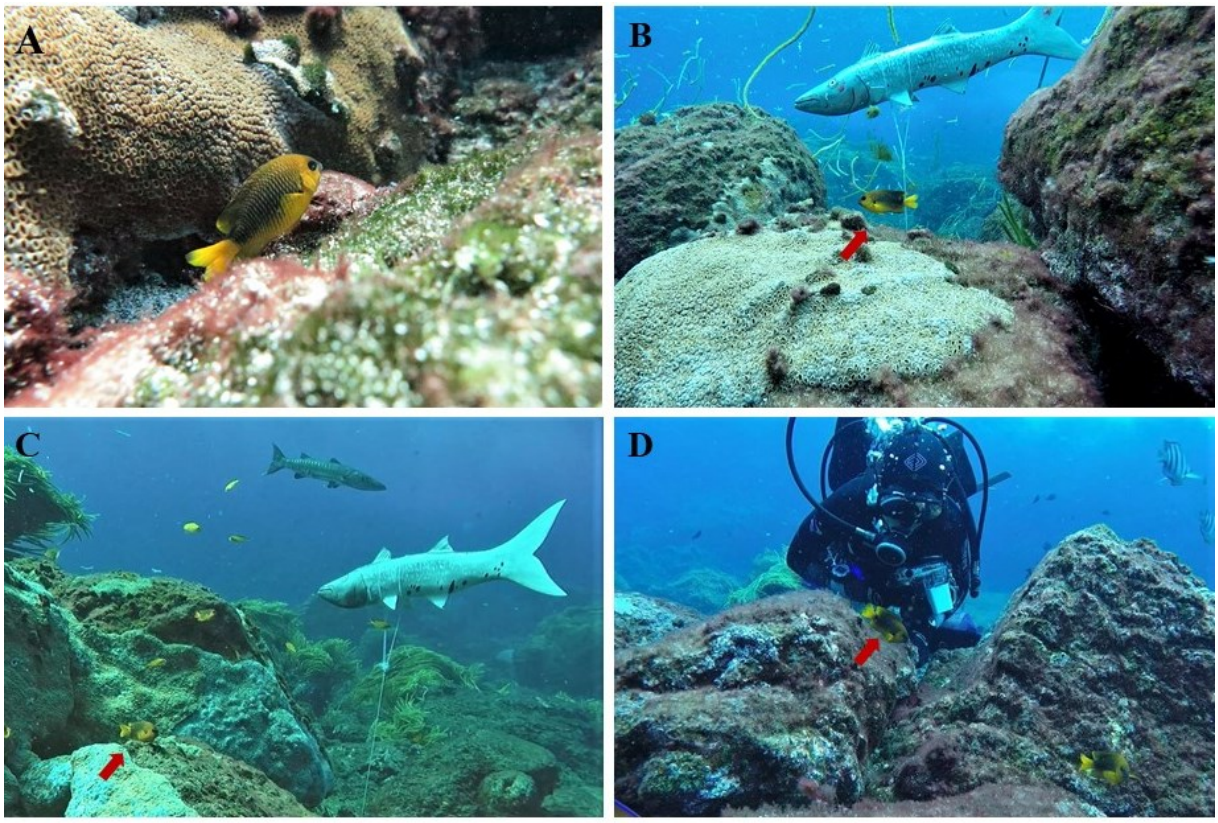


Figure 1: Comparative display of *Stegastes sanctipauli* behaviour in absence of human or reef predator disturbance (A); in the presence of barracuda model (B); an occasional encounter between a reef predator, *Sphyraena barracuda,* and predator model (C); and in SCUBA diver presence (D). Red arrows highlight individuals under study.

On a global perspective, we observed an analogous threat-sensitive response caused by diver presence, once damselfishes have decreased their foraging rates (Benevides et al. 2019; Chapter 2; this work). At one of the most intensively visited recreational Brazilian reef, individuals of *Stegastes fuscus* demonstrated differences in foraging rates between diver presence *vs* absence (PERMANOVA – Pseudo-t: 5.24/ *p: 0.00*), decreasing their feeding rates more than three times (Fig.2B). Likewise, at the popular recreational island reef in Magnetic Island - Australia, *Pomacentrus wardi* reduced approximately four times and *Stegastes apicalis* reduced about twice its foraging when disturbed by the diver (Fig.2C, D respectively).

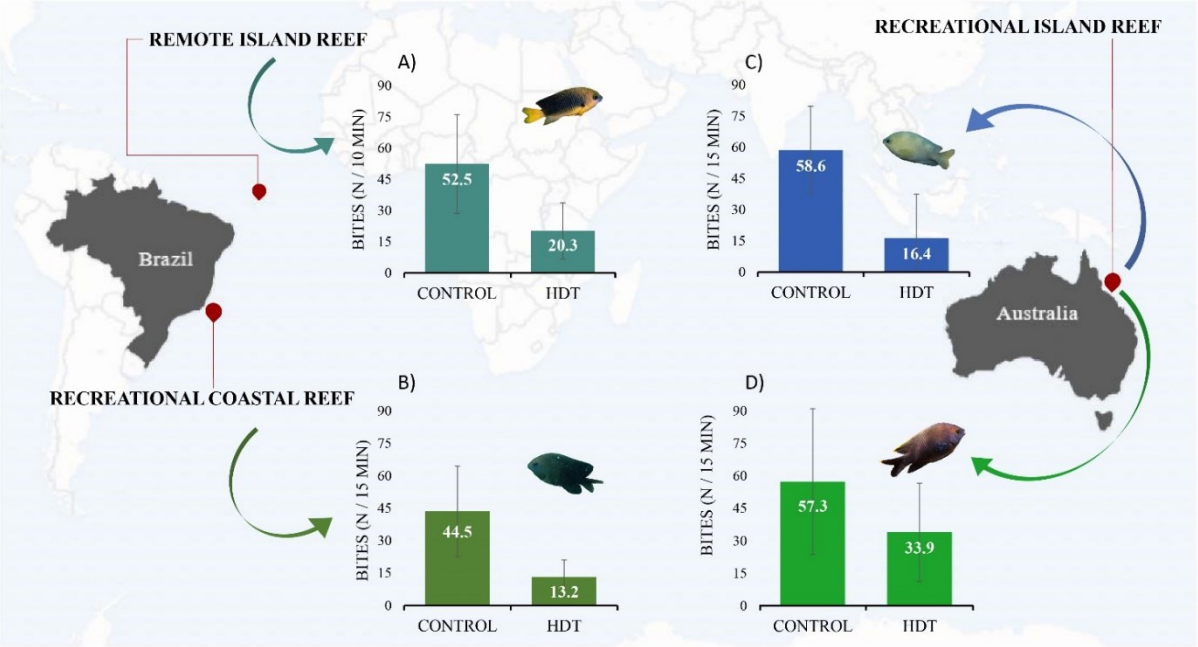


Figure 2: Foraging rates of the damselfishes: *Stegastes sanctipauli* (A), *Stegastes fuscus* (B), *Pomacentrus wardi* (C) and *Stegastes apicalis* (D) under human disturbance treatment – HDT and control, in three distinct reef systems: remote island reef – SPSPA (A), a recreational coastal reef - Arraial do Cabo, RJ – Brazil (B) and recreational mainland island reef - Magnetic island – Australia (C, D).

Animal distraction and interruptions on foraging behaviour are common on natural ecosystems (e.g. with the presence of a threat, competitors or changing in environment conditions). Such behavioural rupture interferes on how to obtain information about optimal decision making, in terms of time and energy allocation, and resources use (Dall, Mcnamara, and Cuthill 1999). Nevertheless, the impairment of foraging may decrease body condition or even induce 'sustained psychological stress', albeit the cognitive and emotional process of avoiding predation still need to be accurate (Clinchy, Sheriff, and Zanette 2013). Therefore, as the results herein suggest, if diver presence interrupts damselfishes' exploration of food resources as do predator presence, then our intimidation in reefs may have a strong influence on fish fitness (by reducing energy intake and consequently the energy used for reproductive success) and/or on community dynamics (by disturbing damselfish functional role on reefs).

Damselfishes are keystone species in marine ecosystems, determining the structure of algal assemblages, patterns of coral zonation, and influencing grazing activities of roving herbivorous fishes (Ceccarelli, Jones, and McCook 2001). This fear-driven reductions in bite rates among damselfish species would consequently imply in a negative effect on successional pathways, decreasing the selective feeding and removal of specific primary producers, thereupon, impacting coral reefs

trophodynamics. For instance, a diminishment on selective algal removal could attract grazers fishes (e.g. parrotfish and surgeonfish), which frequently invade damselfish territories competing for food resources (Schacter et al. 2014), altering herbivory patterns and modifying coral settlement, growth and survival. Importantly, this prospect in the light of fear-driven disturb ought to be carefully considered. Other variables, such as environmental features (e.g. structural complexity) may interact with predator detection and differently influence the outcome of foraging decisions (Catano et al. 2016). However, although our data set does not include environmental data, we considered the same biotic and abiotic conditions to compare the risk-perception through behavioural displays of each species, revelling marked differences between diver presence and control.

By stimulating costly defensive strategies, the intimidation of predators are generally as strong as or stronger than direct consumption, being able to reduce prey density (by decreasing energy intake, offspring and survival) and/or prey activity (foraging effort) (Preisser, Bolnick, and Benard 2005). Perceive humans as predators and respond to it negatively is not anymore a surprising behaviour in wildlife animals, including reef fishes (Ciuti et al. 2012; Frid and Dill 2002; Knight and Temple 1995). Beyond foraging differences, an increase in refuge response of *S. fuscus, S. apicalis* and *P. wardi* during the encounter with a diver was previously observed (Benevides et al. 2019; Chapter 2). Diver behaviour towards damselfish may have a strong influence on how these fish behave under disturbance, rapidly learning avoidance responses to our transient predator-like threat. Accordingly, we should also broaden the knowledge about evolutionary (i.e. through generations) consequences of human NCEs on territorial fishes. It would better predict the implications for the resilience of coral reefs, which have already been dealing with others direct and indirect impact of human activities in coastal and island ecosystems (Madin et al. 2016).

Our study demonstrated the potential influence of human intimidation through non-lethal activities for determining behavioural changes on damselfishes in pristine and recreational areas. Similar to the risk of reef predators, human presence in reef systems can fluctuate greatly in space and time (e.g. daily or seasonally) and these territorial fish have been shown to adjust their behaviour to avoid exposure to unexpected approaches by a diver. Since cumulative effects of foraging decisions can alter community dynamics and ecosystem process (Madin, Gaines, and Warner 2010; Rizzari et al. 2014), we emphasized the potential consequences of those interruptions

on damselfishes foraging behaviour for coral reefs under human disturbance. Ultimately, we also encourage more sustainable diving. Environmental decision-makers must draw attention to unappropriated tourists' behaviour during underwater activities. In turn, it would change cultural values about how to enjoy contact with wildlife, reducing the disturb toward marine organisms. Observation of fish behavioural shifts can show clear signs of distress. Staying with the eyes wide open to those signs will improve conservation efforts and provide future expansion of ethology science.

Acknowledgements

We thank the projects: ‘Long-Term Ecological Research of Brazilians Oceanic Islands’– PELD/ILOC (CNPq 403740/2012-6), and ‘Reef fish under diver influence: behavioural changes and subsidies for the management of underwater tourism’ (FAPEAL 60030 01270/2017) for the logistic and financial support. We also thank Brazilian Navy and “Alfa” boat crew for the logistic support; Caio Pimentel, Moysés Barbosa and Thayná Mello for all help during fieldwork in St. Peter and St. Paul Archipelago. L. J. B. was supported by CAPES, Higher Education Personnel Improvement Coordination – Brazil.

References

Anderson, M., R.N. Gorley, and R.K. Clarke. 2008. PRIMER-E *PERMANOVA + for PRIMER: Guide to Software and Statistical Methods*. Plymouth, UK.

Benevides, Larissa J. et al. 2019. “Fear-Induced Behavioural Modifications in Damselfishes Can Be Diver-Triggered.” *Journal of Experimental Marine Biology and Ecology* 514–515: 34–40. https://linkinghub.elsevier.com/retrieve/pii/S0022098118305550.

Catano, Laura B. et al. 2016. “Reefscapes of Fear: Predation Risk and Reef Heterogeneity Interact to Shape Herbivore Foraging Behaviour” ed. John Fryxell. *Journal of Animal Ecology* 85(1): 146–56. http://doi.wiley.com/10.1111/1365-2656.12440.

Catano, Laura B., Mark B. Barton, Kevin M. Boswell, and Deron E. Burkepile. 2017. “Predator Identity and Time of Day Interact to Shape the Risk-Reward Trade-off for Herbivorous Coral Reef Fishes.” *Oecologia* 183(3): 763–73.

Ceccarelli, Daniela M., Geoffrey P. Jones, and Laurence J. McCook. 2001. “Territorial Damselfishes as Determinants of the Structure of Benthic Communities on Coral Reefs.” In *Oceanography and Marine Biology: An Annual Review*, ed. Taylor & Francis. London: CRC Press, 355–89. https://www.taylorfrancis.com/books/9780203247198.

Ciuti, Simone et al. 2012. “Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear.” *PLoS ONE* 7(11).

Cleveland, Ann. 1999. “Energetic Cost of Agonistic Behavior in Two Herbivorous Damselfishes.” *Copeia* 4(4): 857–67.

Clinchy, Michael, Michael J. Sheriff, and Liana Y. Zanette. 2013. “Predator-Induced Stress and the Ecology of Fear” ed. Rudy Boonstra. *Functional Ecology* 27(1): 56–65.

Dall, Sasha R.X., John M. Mcnamara, and Innes C. Cuthill. 1999. “Interruptions to Foraging and Learning in a Changing Environment.” *Animal Behaviour* 57(1): 233–41.

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. “The Unique Ecology of Human Predators.” *Science* 349(6250): 858–60.

Ferrari, M. C O, Andrew Sih, and Douglas P. Chivers. 2009. “The Paradox of Risk Allocation: A Review and Prospectus.” *Animal Behaviour* 78(3): 579–85. http://dx.doi.org/10.1016/j.anbehav.2009.05.034.

Friard, Olivier, and Marco Gamba. 2016. “BORIS: A Free, Versatile Open-Source Event-Logging Software for Video/Audio Coding and Live Observations.” *Methods in Ecology and Evolution* 7(11): 1325–30.

Frid, Alejandro, and Lawrence Dill. 2002. “Human-Caused Disturbance Stimuli as a Form of Predation Risk.” *Conservation Ecology* 6(1): 1–12. http://www.consecol.org/vol6/iss1/art11/.

Giglio, Vinicius J. et al. 2018. “Large and Remote Marine Protected Areas in the South Atlantic Ocean Are Flawed and Raise Concerns: Comments on Soares and Lucas (2018).” *Marine Policy* 96(May): 13–17. https://doi.org/10.1016/j.marpol.2018.07.017.

Huddart, David. 2019. “Recreational Scuba Diving and Snorkelling.” In *Outdoor Recreation*, eds. David Huddart and Tim Stott. Cham, Switzerland: Springer International Publishing, 361–94. http://link.springer.com/10.1007/978-3-319-97758-4_14.

Januchowski-Hartley, F. A. et al. 2011. “Fear of Fishers: Human Predation Explains Behavioral Changes in Coral Reef Fishes” ed. Julian Clifton. *PLoS ONE* 6(8): e22761. https://dx.plos.org/10.1371/journal.pone.0022761 (May 6, 2014).

Jones, Geoffrey P. Gp, Lara Santana, Laurence J. Lj McCook, and Mi Mark I. McCormick. 2006. “Resource Use and Impact of Three Herbivorous Damselfishes on Coral Reef Communities.” *Marine Ecology Progress Series* 328(2001): 215–24.

Kaufmann, John H. 1983. “On the Definitions and Functions of Dominance and Territoriality.” *Biological Reviews* 58(1): 1–20. http://doi.wiley.com/10.1111/j.1469-185X.1983.tb00379.x.

Kelley, Jennifer L., and Anne E. Magurran. 2003. “Learned Predator Recognition and Antipredator Responses in Fishes.” *Fish and Fisheries* 4(3): 216–26. http://doi.wiley.com/10.1046/j.1467-2979.2003.00126.x.

Knight, R.L., and S.A. Temple. 1995. “Origin of Wildlife Responses to Recreationists.” In *Wildlife and Recreationists: Coexistence through Management and Research*, eds. R.L. Knight and K.J. Gutzwiller. Washington, DC: Island Press, 81–91.

Madin, Elizabeth M. P. et al. 2016. “Human Activities Change Marine Ecosystems by Altering Predation Risk.” *Global Change Biology* 22(1): 44–60. http://doi.wiley.com/10.1111/gcb.13083.

Madin, Elizabeth M P, Steven D. Gaines, and Robert R. Warner. 2010. “Field Evidence for Pervasive Indirect Effects of Fishing on Prey Foraging Behavior.” *Ecology* 91(12): 3563–71.

Magalhães, Gabriela Machado et al. 2015. “Changes in Benthic Communities along a 0-60 m Depth Gradient in the Remote St. Peter and St. Paul Archipelago (Mid-Atlantic Ridge, Brazil).” *Bulletin of Marine Science* 91(3): 377–96.

Matassa, Catherine M., Sarah C. Donelan, Barney Luttbeg, and Geoffrey C. Trussell. 2016. “Resource Levels and Prey State Influence Antipredator Behavior and the Strength of Nonconsumptive Predator Effects.” *Oikos* (January): 1–11.

Nunes, José Anchieta C.C. et al. 2019. “Reef Fish Antipredator Behavior in Remote Islands Does Not Reflect Patterns Seen in Coastal Areas.” *Ethology Ecology & Evolution* 0(00): 1–11. https://www.tandfonline.com/doi/full/10.1080/03949370.2019.1636141.

Pinheiro, Hudson T. et al. 2018. “South-Western Atlantic Reef Fishes: Zoogeographical Patterns and Ecological Drivers Reveal a Secondary Biodiversity Centre in the Atlantic Ocean” ed. Eric Treml. *Diversity and Distributions* 24(7): 951–65. http://doi.wiley.com/10.1111/ddi.12729.

Preisser, Evan L., Daniel I. Bolnick, and Michael F. Benard. 2005. “Scared to Death? The Effects of Intimidation and Consumption in Predator-Prey Interactions.” *Ecology* 86(2): 501–9. http://doi.wiley.com/10.1890/04-0719.

Rizzari, Justin R., Ashley J. Frisch, Andrew S. Hoey, and Mark I. McCormick. 2014. “Not Worth the Risk: Apex Predators Suppress Herbivory on Coral Reefs.” *Oikos* 123(7): 829–36.

Schacter, Carley R. et al. 2014. “Risk-Sensitive Resource Defense in a Territorial Reef Fish.” *Environmental Biology of Fishes* 97(7): 813–19.

Triki, Zegni, and Redouan Bshary. 2019. “Long-Term Memory Retention in a Wild Fish Species Labroides Dimidiatus Eleven Months after an Aversive Event.” *Ethology* (August): 1–5.

V. CONCLUSÕES GERAIS

Por meio do conceito de “paisagem do medo”, este trabalho discute as diferentes respostas comportamentais que peixes territoriais podem exibir frente a variações na percepção do risco, na presença e ausência do mergulhador. De modo geral, quatro espécies de peixes territoriais alteraram a percepção do risco em relação à presença do mergulhador, reduzindo as taxas de forrageamento, elevando a busca por refúgio e/ou reduzindo a defesa do território. Particularmente, no primeiro capítulo, verificou-se que tanto o mergulhador ‘SCUBA’ quanto ‘snorkel’ perturbaram o comportamento de indivíduos de *Stegastes fuscus* de forma correspondente, em um recife frequentemente visitado, na costa sudeste do Brasil. No segundo capítulo, a presença do mergulhador prejudicou similarmente o comportamento de espécies que coexistem em um recife em ilha costeira na Austrália, incluindo redução no tempo que os indivíduos de *S. apicalis* e *Pomacentrus wardi* destinavam com a patrulha de seus territórios. No terceiro capítulo, a espécie endêmica do remoto Arquipélago de São Pedro e São Paulo, *S. sanctipauli,* apresentou similares respostas comportamentais frente a presença do mergulhador e do modelo de predador, *Sphyraena barracuda*, sugerindo que esses peixes podem não distinguir ambas ameaças efetivamente. Além disso, observou-se uma resposta análoga entre peixes territoriais que habitam os distintos sistemas recifais, onde houve significativa redução nas taxas de forrageamento quando o mergulhador estava presente ao redor dos territórios.

Por fim, esta tese destaca que alterações comportamentais em peixes territoriais podem ter potenciais efeitos para a condição corporal dos indivíduos bem como para as relações tróficas no ambiente marinho. Ao perceber humanos como ameaça, mesmo sem o efeito-letal, peixes territoriais reduzem a alimentação e/ou o cultivo seletivo de algas. Consequentemente, isso poderá alterar as taxas de herbivoria por outras espécies, afetando processos ecológicos e a dinâmica da comunidade recifal. Destaca-se aqui, a importância de ampliar os experimentos para longo-prazo, devido aos possíveis efeitos cumulativos desencadeados por mergulhadores. Alterações no comportamento de peixes territoriais podem ser indicadores de distúrbio, favorecendo ações para o manejo do mergulho recreativo. Além disso, contribuem para ampliação do conceito de ‘paisagem do medo’, incluindo o efeito não-letal da presença humana na percepção do risco em espécies com reduzida capacidade de distribuição espacial.