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Reviews

An overview of ecological traps in marine ecosystems

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Running heads:

SE Swearer *et al.*

Ecological traps in marine ecosystems

Humans are altering marine ecosystems at unprecedented rates, and these changes can result in animals selecting poor-quality habitats if the cues they use become misleading. Such "ecological traps" increase extinction risk, reduce ecosystem resilience, and are a consequence of human-induced rapid environmental change. Although there is growing evidence for traps impacting terrestrial species, the phenomenon has so far received little attention from marine scientists. To explore why so few studies have attempted to identify traps in the ocean, we conducted a literature review of the major drivers of marine environmental change to determine how their impacts on habitat choice and species fitness are being assessed. From this we summarize the current evidence for marine traps, present case studies to show why the phenomenon is potentially common in the ocean, highlight ways to advance awareness and understanding of traps, and demonstrate how this information can help improve management of marine environments.

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In a nutshell:

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- Ecological traps form when animals are attracted into poor-quality habitats where their fitness is compromised
- Human modification of terrestrial habitats creates ecological traps for terrestrial animals, but there is little evidence that alterations to marine habitats cause such traps for marine animals
- Using case studies and a literature review, we summarize the current evidence for marine ecological traps, and highlight the types of species traits and behaviors associated with greater susceptibility to traps
- We conclude that traps are potentially a common but under-researched phenomenon in marine ecosystems, and provide guidance on how best to identify them and manage their impacts

Given that nearly 40% of the Earth's seven billion people live within 100 km of a coastline (Sale *et al.* 2014), it is unsurprising that the human impact on the world's oceans is considerable, with marine species and habitats having long experienced the detrimental effects of a range of environmental threats (Kappel 2005). For example, oceans are warming in response to climate change; non-native species have been introduced; many fisheries have declined or collapsed; and the structure of food webs has been altered, in some cases irreversibly (Halpern *et al.* 2008). Over the past decade, such human-induced impacts have intensified across nearly 70% of the world's oceans (Halpern *et al.* 2015). Although the extent of these changes is astonishing, a key challenge for animals is that humans are altering ecosystems at faster rates than natural processes, a phenomenon commonly referred to as human-induced rapid environmental change (HIREC; WebTable 1; Sih *et al.* 2011). HIREC in the ocean encapsulates a range of biological, chemical, and physical changes that arise from a diversity of causes, including both protective (eg marine parks) and exploitative (eg fishing) management practices, pollution, introduced and invasive species, habitat modification resulting from the construction of marine infrastructure (eg reefs, piers, aquaculture and coastal structures) and climate change (Figure 1). Although some of these changes might benefit some animals (eg offshore oil rigs being one of the most productive marine fish habitats globally; Claisse *et al.* 2014), many are likely to have negative effects on animals, either directly (eg mortality caused by oil spills; Peterson *et al.* 2003) or indirectly (eg climate change altering the strength of interspecific interactions; Milazzo *et al.* 2013).

Changes in behavior are often one of the first ways that animals respond to HIREC, and behavioral plasticity has allowed some species (eg urbanized or invasive species) to adapt to and even thrive under novel conditions (Wong and Candolin 2015). However, many animals fail to adapt, and consequently their fitness (ie growth, survival, and reproduction) is compromised (Robertson *et al.* 2013). These effects are likely to be even more severe if animals are no longer able to identify and respond appropriately to threatening situations.

Many animals use environmental cues to select habitats that maximize their fitness. However, HIREC can mean that the environment changes so quickly that these cues no longer provide a good indication of habitat suitability. In turn, this can lead to the formation of ecological traps – situations whereby animals prefer habitats in which their fitness is lower than it would have been if they had selected another available option (WebTable 1; Robertson and Hutto 2006; Robertson *et al.* 2013). Perhaps the most compelling example of an ecological trap is the attraction of some aquatic insects toward polarized light reflecting from oil spills or artificial surfaces, such as automobiles and gravestones (Horváth *et al.* 2009); insects often die after landing and attempting to lay eggs on these surfaces. Ecological traps arise when the links between habitat quality and habitat selection become decoupled through changes to habitats, settlement cues, or both (Robertson and Hutto 2006). Because traps can increase both local and regional extinction risks (Battin 2004; Hale *et al.* 2015), understanding how they form, how animals respond to them, and how they can be mitigated are important questions in conservation and restoration biology (Battin 2004; Hale and Swearer 2016, 2017).

Ecological traps are most likely to occur in systems where environmental conditions are undergoing rapid change (Battin 2004), potentially leading to a greater likelihood of a mismatch between these conditions and those under which the animal's traits were shaped (Ghalambor *et al.* 2007). There is therefore a strong basis for predicting that ecological traps could affect many marine species. However, ecological traps have primarily been studied in terrestrial habitats, especially in relation to birds in Europe and North America (Hale and Swearer 2016). Prior to the current review, we were aware of only one study that has explicitly demonstrated an ecological trap in the ocean (Table 1; Sherley *et al.* 2017); two studies that tested but did not find that coastal fish farms (Dempster *et al.* 2011) and offshore wind farms (Reubens *et al.* 2013) act as traps; and several studies that provide compelling indirect evidence for potential traps resulting from fish aggregating devices (FADs; Hallier and Gaertner 2008), casitas (small houses for spiny lobsters; Gutzler *et al*. 2015), and reefs with invasive lionfish (*Pterois* spp; Benkwitt 2017).

This limited evidence may reflect that, for logistical reasons, fewer such studies are performed in marine than terrestrial ecosystems (Munguia and Ojanguren 2015), that ecological traps are considered less relevant in marine ecosystems, or that they have been studied but not labelled as such (eg fish fail to avoid polluted sites [Moles *et al.* 1994] and this reduces their fitness [Moles and Norcross 1998]). Alternatively, ecological traps could indeed be uncommon in marine ecosystems. We explored why so few studies have successfully identified ecological traps in marine systems and demonstrate why we believe this likely reflects limited effort to identify traps, rather than the theory not being applicable to marine systems. To do so, we first present case studies and the results of a systematic review of the marine HIREC literature to examine how responses by marine animals to environmental change are investigated, and then summarize the species traits that influence susceptibility to traps and amenability to diagnosing their effects, presenting example taxa for both. Next, we highlight ways to advance awareness and understanding of traps and finally show how this information can be applied to manage their impacts.

Key question 1: are ecological traps relevant to marine ecosystems?

Given the magnitude and scale at which humans have altered the marine environment, there is no reason to believe that marine ecosystems are less susceptible to the formation of ecological traps than terrestrial ecosystems. Indeed, humans have been intentionally creating ecological traps in the sea for millennia; they merely have not been recognized as such. A prime example is octopus trap fishing, a method that has been practiced since at least the 3rd-century CE (based on its depiction in an ancient Roman mosaic from Sidi Abdakkah, Tunisia, that is now in the Bardo Museum in Tunis). This traditional fishing method exploits the proclivity of octopuses to shelter in holes – or suitably sized pots – a type of behavioral exploitation similarly employed in fishing for lobsters (casitas; Gutzler *et al.* 2015) and pelagic piscivorous fishes (FADs mimicking natural flotsam that typically have sheltering bait fish; Hallier and Gaertner 2008), and results in increased mortality. By their very nature, these fishing activities meet the criteria required to demonstrate an ecological trap (Robertson and Hutto 2006): animals prefer habitats (eg lobster pots) in which they experience fitness costs (ie fishing mortality).

Although the mechanisms vary, virtually all marine animals make habitat selection decisions during their lifetime (eg larval settlement [Keough and Swearer 2007], ontogenetic habitat shifts [Huijbers *et al.* 2012], habitat-dependent migration [Sequeira *et al.* 2018]) and are therefore susceptible to ecological traps, regardless of the underlying cause. Some marine animals sequentially assess each habitat they encounter and decide whether to accept or reject and continue searching. Sequential search tactics are often characteristic of species with less capacity for movement, and in time-limited sequential dispersers (eg non-feeding marine invertebrate larvae) acceptance thresholds decline with time (eg the desperate larva hypothesis; Marshall and Keough 2003). If trap habitats are therefore perceived to be above the acceptance threshold, individuals will become trapped and with increasing likelihood over time. In contrast, other animals use comparative approaches to habitat selection, assessing a number of locations before selecting the habitat perceived to be the highest quality (eg a "best-of-*n*" approach; Stamps 2006). These tactics are typically exhibited by species with greater capacity for movement and/or species that are less time limited, such as marine megafauna. For such species, the more habitats assessed, the greater the likelihood of encountering a trap. Regardless of the mechanism underpinning habitat selection, a diversity of marine animals are therefore potentially vulnerable to traps. We illustrate this with several case studies (Table 1) that provide support for the view that ecological traps are a relevant phenomenon to many marine species and environmental contexts.

Key question 2: is the information needed to diagnose marine ecological traps being collected?

There has been considerable work examining the effects of HIREC in the ocean; for example, the Ocean Health Index (www.oceanhealthindex.org) summarizes changes in human impacts across both space and time (Halpern *et al.* 2015). Comprehensive evaluations of the fitness effects of some pressures also exist (eg ocean acidification; Kroeker *et al.* 2010), as well as their potential impacts on behavior (eg ocean acidification, global warming; Nagelkerken and Munday 2016). It is therefore pertinent to ask whether marine ecologists are collecting the information required to identify an ecological trap when studying the effects of HIREC.

Assessing ecological traps requires information about how HIREC affects the fitness and habitat preferences of animals (Robertson and Hutto 2006). What inferences can be made, however, depends on how fitness and preference are measured. Habitat preferences can be assessed using observational (eg population density) or experimental (eg choice experiments; Robertson and Hutto 2006) methods, but purely observational methods, such as population surveys, cannot provide definitive evidence that observed patterns are due to preference and not to other processes (Underwood *et al.* 2004); for example, more fish at a particular reef may simply reflect lower post-settlement mortality rather than habitat preference. Likewise, direct fitness measures (ie survival and reproduction) will provide stronger evidence than indirect ones (eg growth rate, body condition, biomarkers), as these indicators may not result in differences in fitness (Hale and Swearer 2016).

Testing for an ecological trap therefore requires information about the habitat selection behavior of animals and how their fitness differs between habitats. To determine if this information is routinely being collected by researchers characterizing responses to HIREC in the ocean, we conducted a comprehensive literature review by performing Web of Science searches (conducted on 19 September 2019). Because this is a vast area of interdisciplinary research, four sets of search terms (see WebTable 2) were required to initially identify studies most relevant to ecological traps. To be included in the database, studies needed to meet eight criteria (summarized in Panel 1); our search returned 518 studies that met the criteria (see WebPanel 1 for the complete list of studies). We reviewed all of these studies to extract the following information:

(1) which of five forms of HIREC was the focus of the study: climate change, invasive/introduced species, pollution, marine infrastructure (eg piers, wind farms, breakwaters), or management practices (eg fishing, aquaculture, marine reserves);

(2) whether the study measured fitness responses to HIREC, habitat selection behavior, or both fitness and habitat selection;

(3) for studies that measured fitness, if the fitness measures were (i) indirect population level (eg population size, population growth rate), (ii) indirect individual level (eg body condition, growth/development rate and size, biomarkers, morphology including deformities), or (iii) direct (eg survival, reproduction); and

(4) for studies that assessed habitat selection, methods were categorized as (i) observational (eg abundance, distribution of dominant individuals, habitat use, population size variance, site fidelity), (ii) experimental (eg choice experiments), or (iii) both observational and experimental; studies were classified in this way because methods that included experimental approaches were most likely to provide the strongest evidence that observed results were due to preference rather than alternative processes (eg differential post-settlement mortality).

Our results showed that most of these studies examined the effects of management practices on marine animals (39%) in comparison to infrastructure (21%), pollution (19%), invasive/introduced species (12%), and climate change (9%). Overall, only 17% of studies measured both fitness and preference (Figure 2). Of the 268 studies that measured preference, only 32% used experimental methods. In addition, fitness effects were often only measured indirectly (74% of studies), and a mere 3.4% of studies (18 studies) combined experimental tests of preference and direct estimates of fitness that would provide the strongest evidence to assess a potential ecological trap. Of these 18 studies, five detected no or unclear fitness differences among habitats, whereas of the remaining 13, six found evidence consistent with an ecological trap and seven found evidence for adaptive habitat selection (see WebTable 3 for a summary of these studies). Our review also revealed that HIREC was most commonly studied from the perspective of examining effects on fish, a trend consistent across the major forms of HIREC, with the exception of invasive species, for which mollusks were the most commonly studied taxon (WebFigure 1). These results strongly suggest that the information required to properly identify ecological traps is rarely collected in studies of the effects of HIREC in marine environments, but when such information is collected, there is a reasonable chance of detecting traps.

Key question 3: why and where should ecological traps be studied in the ocean?

Because ecological trap theory was originally developed with regards to terrestrial birds, it may have largely escaped the attention of marine ecologists. Regardless of the reason, a comprehensive understanding of ecology depends on testing theories in different systems to identify similarities or differences (Borer *et al.* 2014). Expanding research on ecological traps to have a greater marine focus will provide more targeted information about fitness and habitat selection, which will improve our understanding of how marine animals respond to HIREC. This will be particularly important if, for example, marine traps can arise in ways that differ from terrestrial traps (Hale and Swearer 2016).

However, fundamental differences between terrestrial and marine ecosystems (Carr *et al.* 2003) may make it more difficult to diagnose traps in the ocean. For instance, it may be easier to access terrestrial study sites (Munguia and Ojanguren 2015) and directly observe or tag terrestrial animals to collect information about habitat preference and fitness. In contrast, dispersal and habitat selection for many marine taxa, particularly benthic species, often occur early in life, when individuals (eg larvae) are often small and hard to track or observe (Keough and Swearer 2007), although these same traits make them more amenable to assessing habitat preference and fitness in a laboratory setting. Even with methodological advancements that have greatly improved our understanding of the movement ecology of marine larvae, such as elemental fingerprinting (Thorrold *et al.* 2007), DNA parentage (Almany *et al.* 2017), and increasingly complex biophysical models (Swearer *et al.* 2019), direct observations remain logistically challenging, particularly at the end of the larval period when individuals make habitat selection decisions. Consequently, it may be more fruitful to initially focus on species whose movements can be tracked (eg marine megafauna) or those for which habitat selection behaviors can be directly observed (eg reef fish at settlement). Indirect methods (eg quantifying temporal variations in population size) may need to be relied upon for other species for the time being, with the understanding that such methods provide less certainty that observed patterns reflect preference as opposed to differences in survival.

The choice of species will also depend on a taxa's susceptibility to traps and the associated fitness consequences. We have previously shown that the effects of (primarily terrestrial) ecological traps on habitat selection and fitness vary in terms of the cause and the affected taxa (Hale and Swearer 2016). How vulnerable a species is to falling into a trap will depend on the probability of encountering the trap and the likelihood of selection. This will, in part, depend on an animal's movement/dispersal capacity and the sensitivity of its sensory systems (ie the distances over which habitat cues can be detected and evaluated). How susceptible a species is to the fitness costs associated with a trap will depend on its life history. Species with limited adaptive potential (ie slow rate of evolution, low capacity for learning, no behavioral adaptations to change) or limited reproductive capacity (ie small populations, low fecundity, long reproductive cycles) will be particularly vulnerable (Hale *et al.* 2015). Therefore, the greatest opportunities for future work will be on species that are highly susceptible (Figure 3), but that can also be feasibly studied (Figure 4).

Key question 4: would research on ecological traps provide information useful for managing and conserving marine ecosystems?

Due to the widespread effects of HIREC on marine ecosystems, various management initiatives have been employed to mitigate negative impacts. For instance, marine protected areas are dedicated to conserving important natural areas. Where habitats have been lost, restoration is undertaken to re-establish abiotic conditions and key habitat-forming species, such as those that form mangrove forests, saltmarshes, and shellfish reefs. Artificial reefs (ARs) are commonly deployed to enhance fisheries and mitigate impacts to natural reef habitat. In addition, ecological engineering is used to "green" infrastructure built along the coast (eg seawalls, breakwaters) and offshore (eg oil rigs, wind farms). For example, marine eco-engineering can involve redesigning or retrofitting microhabitats to structures (eg pits, crevices, water-retaining features) to increase surface complexity for species colonization (Chapman and Underwood 2011). Although such management practices are implemented with good intentions, they could inadvertently have negative effects if they result in ecological traps (Figure 5; Hale and Swearer 2016).

Restoration and ecological engineering may create habitats that animals prefer but which reduce their fitness, therefore resulting in an ecological trap. For instance, ARs may either increase fish production or simply attract individuals from elsewhere (Bohnsack 1989), but regardless of the mechanism, fish inhabiting ARs may be more susceptible to harvesting, given that ARs are often deployed to enhance fishing (Feary *et al.* 2011). The design of ARs can also influence whether they produce persistent assemblages or potentially function as ecological traps. Reefs with large shelters, for example, will attract and benefit big predatory fish, but without small shelters the abundance of prey fish decreases (Hixon and Beets 1989). This could cause an ecological trap, as prey fish will experience greater mortality if they are attracted to ARs that lack the smaller shelters required for protection (eg Komyakova and Swearer 2019). Likewise, ecologically engineering seawalls by adding microhabitats may increase the colonization of intertidal species, but if the created habitats or the surrounding seawall does not provide the appropriate habitat for these species, survival or reproduction may be reduced. Indeed, the reproductive output of some intertidal gastropods is lower on seawalls (Moreira *et al.* 2006).

As anthropogenic modification of marine habitats continues, incorporating ecological principles to maintain diversity and ecological functioning will become increasingly important. This process will be assisted by a better understanding of how ecological traps form in the marine environment and by an evaluation of the fitness consequences of creating, modifying, or restoring habitat, both of which will ultimately improve management of HIREC, as evaluating whether management practices are unintentionally creating traps is an essential step toward enhancing outcomes for animals (Hale and Swearer 2017).

Conclusions and future directions

Although ecological traps have been studied in terrestrial systems since the 1970s, with an upsurge in research over the past decade, the concept has rarely been applied to marine ecosystems. We suggest this is likely due to two misconceptions: that traps are not applicable to marine systems and that they are already being studied under other guises. We have demonstrated here that ecological traps are relevant to marine systems and that current attempts to quantify the impacts of HIREC in the ocean often do not collect the required information on habitat selection behavior and the resultant impacts on fitness.

Research to date has focused primarily on identifying traps, with less work on scaling up from individual behavior and performance to landscape scales. Although it is important that studies are undertaken to identify traps with a diverse range of marine taxa, in order to improve understanding of the potential prevalence of this problem and to identify species most at risk, greater effort is needed at scaling up from individual behavior and performance to landscape-scale population and community responses (eg Hale *et al.* 2015). The drivers of HIREC operate over large spatial scales and it will be important to consider the extent of these changes in relation to the scales of movement of marine taxa. In some instances, scales of impact may be so extensive that many individual animals will be forced to choose between habitats that are all of poor quality. Where to prioritize habitat restoration/creation to maximize the benefits to animal populations will require knowledge of movement and habitat selection behavior across the landscape.

The rate and extent of HIREC in the ocean is increasing (eg Halpern *et al.* 2008, 2015) and the environment is changing in ways that likely mean ecological traps will be more prevalent in the future. For example, climate-change stressors can cause marine species to alter their responses to cues that are used to select habitats (Nagelkerken and Munday 2016). In addition, light pollution (Davies *et al.* 2014) and noise pollution (Cox *et al*. 2018), which can have pervasive effects on behavior, are both rapidly increasing in marine systems. Considering animal responses to HIREC will also be important if, for instance, species that shift their ranges in response to climate change encounter ecological traps more frequently because their phenotype is mismatched to the new environment (Hale *et al*. 2016). A greater awareness of the potential for ecological traps and their underlying drivers, how these affect animals, and how they can be mitigated will be crucial for understanding how HIREC affects marine animals, and for guiding current and future conservation, restoration, and management actions.

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Supporting Information

Additional, web-only material may be found in the online version of this article at

Figure captions

Figure 1. Five major types of human-induced rapid environmental change (HIREC) have been identified: habitat modification, spread of invasive species, harvesting by humans, pollution, and climate change (Sih *et al.* 2011). Examples of these in marine systems include (a) built infrastructure, which replaces and fragments natural habitats; (b) the invasive Northern Pacific seastar (*Asterias amurensis*); (c) trawl fishing; (d) stormwater runoff; and (e) coral bleaching.

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(d) Water Environment Federation
(e) The Ocean Agency/XL Catlin Seaview Survey

Figure 2. Results of a literature review undertaken to document how the effects of HIREC are studied in the ocean. We reviewed 518 studies and recorded if (a) they measured effects on the fitness of animals (Fit), on habitat preference (HS), or on both fitness and preference (Both). We also examined whether (b) studies that examined habitat preference used observational (Obs) or experimental (Exp) methods, and (c) studies that examined fitness used direct (eg mortality – Direct) measures or indirect individual (Ind) or population (Pop) level measures. See Panel 1 and WebTable 2 for full details of the review methodology. Note that the sum of all bars in each panel is larger than the 518 studies reviewed, given that

papers may be scored in more than one category; for example, in (c), any one study could have included more than one Direct, Indirect (individual), or Indirect (population) measure of fitness.

Figure 3. Example species and associated life-history traits that influence the likelihood of selecting traps or experiencing fitness-related consequences. Assessing vulnerability to ecological traps will need to adopt an integrated-trait approach, as species are likely to have traits that will increase both vulnerability and resilience (framework modified from Batten 2004; Hale *et al*. 2015; Hale and Swearer 2016).

Figure 4. Example species and associated life-history traits that influence the feasibility of studying habitat selection or fitness consequences. Identifying amenable species should consider methodologies that will facilitate collection of data on both habitat preference and fitness: for example, the use of satellite tags on marine megafauna that can measure both habitat use and survival (framework modified from Batten 2004; Hale *et al*. 2015; Hale and Swearer 2016).

Figure 5. Hypothetical scenarios of how ecological traps caused by management practices might affect a coastal ecosystem. (left) Illustration of the intended outcomes of four types of activities: (1) replanted mangroves that provide high-quality habitat where birds can breed, (2) eco-engineered structures that provide habitat where starfish can survive, and artificial reefs that increase production of (3) prey fish and (4) predatory fish. Animals prefer these higher quality habitats. (right) However, if these habitats are ecological traps, they will be preferred but animals will experience reduced fitness if, for example (1) replanted mangroves do not support production of prey fish and birds fail to breed, (2) eco-engineered structures fail to provide refuge from desiccation and starfish do not survive, (3) artificial reefs do not provide shelter for prey fish that then experience increased predation, and (4) fish are attracted to artificial reefs where they are caught by fishers.

Table 1. Examples of potential or demonstrated marine ecological traps for each type of human-induced rapid environmental change (HIREC)

Type of HIREC	Impacted species	Potential for trap	Evidence from study	Tested for trap?	Trap found?	References
Habitat modification	Atlantic cod (*Gadus morhua*), saithe (*Pollachius virens*)	Attraction to marine infrastructure (sea-cage fish farms) that provides low-quality habitat	Improved body and liver condition in fish attracted to farms	Yes	No	Dempster *et al.* (2011)
Invasive species	Sydney cockle (*Anadara trapezia*)	Preferential recruitment to the invasive green alga *Caulerpa taxifolia*, which provides low-quality habitat	Lower survival and female reproduction; large recruitment of juveniles to alga but no preference	No	–	Gribben and Wright (2006); Wright and Gribben (2008)
Management practices	Skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*)	Attraction to fish aggregating devices (FADs) reduces fitness	Greater percentage of empty stomachs, reduced growth rate and size in FAD-caught tuna	No	–	Hallier and Gaertner (2008)
Pollution	Loggerhead sea turtles (*Caretta caretta*)	Artificial lighting attracts turtle hatchlings landward, reducing survival	Crawling toward an artificial light source impaired the ability of hatchlings to swim offshore	No	–	Lorne and Salmon (2007)
Climate change	African penguins (*Spheniscus demersus*)	Climate change and fishing induced shift of prey fish, resulting in poor-quality feeding grounds preferred by juvenile penguins	Reduced survival of juveniles that selected degraded habitats to forage	Yes	Yes	Sherley *et al.* (2017)

Panel 1. The eight criteria required for a study to be included in the review

(1) Presented empirical data (ie empirical study or modeling study with some data collection).

(2) Worked in marine habitats, defined by tidal influence; this includes brackish habitats, sea ice, and beaches below the vegetation line.

(3) A form of human-induced rapid environmental change (HIREC) must have occurred; this includes natural phenomena that increase in frequency or severity under HIREC (eg eutrophication, high temperatures, anoxia).

(4) The HIREC event must have occurred prior to habitat selection, so that animals are responding to a changed environment; for example, studies reporting fish population declines and destruction of benthos by trawling were excluded, but studies that characterized habitat preferences or fitness of fauna that recruit to previously trawled areas were included.

(5) The study must have focused on a defined area or habitat that an animal can avoid; for example, studies that focused on the effects of climate change on either habitat selection or the loss/gain of habitats were included (eg looking at fitness/habitat selection in relation to bleached/unbleached habitats), whereas studies that looked at the fitness costs of global changes in climate (eg increased sea-surface temperature, ocean acidification) were excluded.

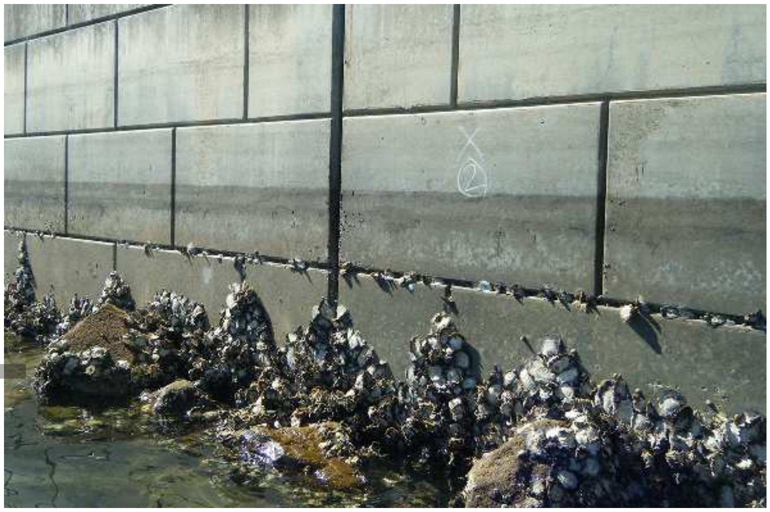
(6) Invasive species were only considered relevant if they were habitat formers or modifiers, or if the study tested whether the presence of an invasive predator/prey/competitor altered the quality of a habitat for native species.

(7) Studies had to have a comparison against which fitness/preference responses to HIREC affected habitats could be assessed; this included spatial/temporal gradients, before–after, control–impact, and before–after control–impact designs; laboratory studies were included if they measured responses to realistic variables associated with HIREC.

(8) Studies had to have either individual-level data on habitat selection decisions or fitness measures, or population-level data on abundance, population growth, biomass, or density; studies that focused on community/assemblage level responses were excluded, given that these sorts of responses could be attributed to a wide variety of factors (ie it was difficult/impossible to assign any response to HIREC).

Swearer - Figure 1 mockup

Please arrange Figure 1 (a)-(e) as shown below with each component the same size, and add labels (a)-(e) as per style.



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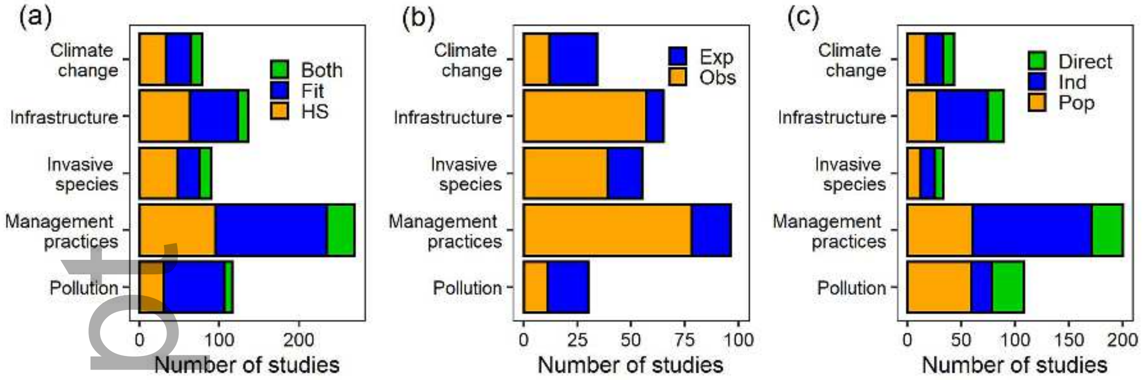

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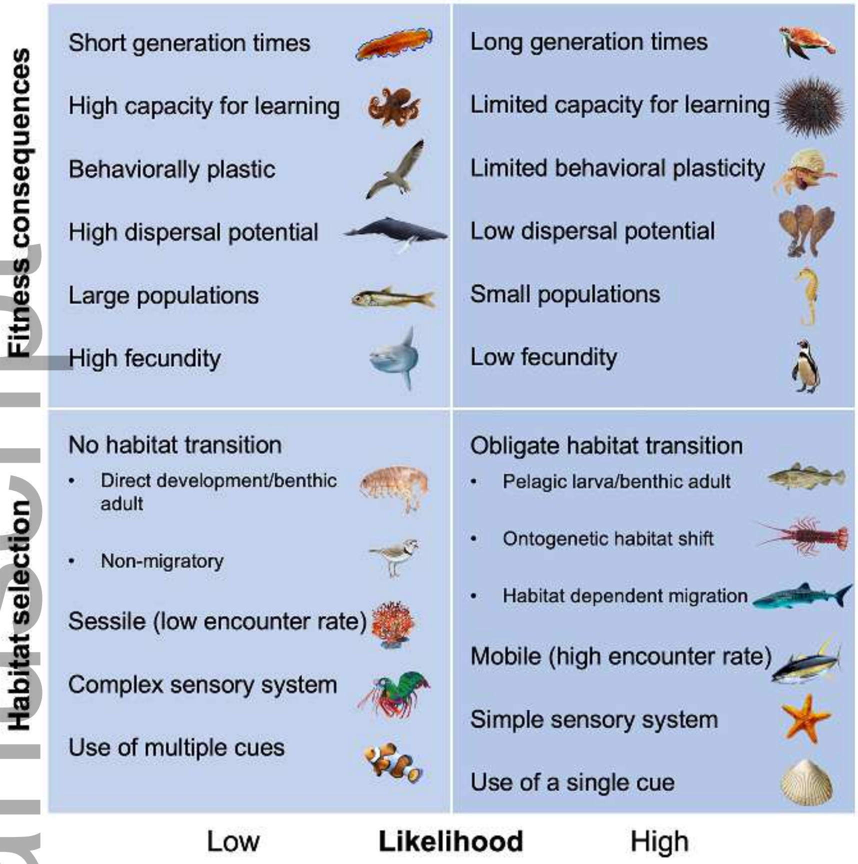
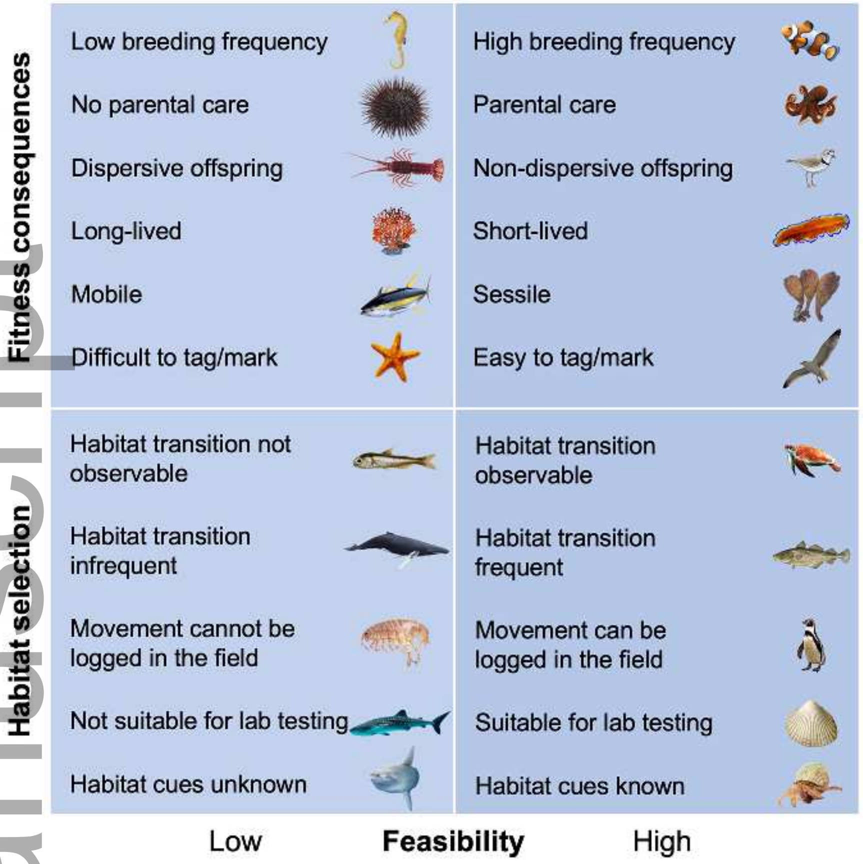

Fitness consequences
Short generation times
High capacity for learning
Behaviorally plastic
High dispersal potential
Large populations
High fecundity
Long generation times
Limited capacity for learning
Limited behavioral plasticity
Low dispersal potential
Small populations
Low fecundity
Habitat selection
No habitat transition
• Direct development/benthic adult
• Non-migratory
Sessile (low encounter rate)
Complex sensory system
Use of multiple cues
Obligate habitat transition
• Pelagic larva/benthic adult
• Ontogenetic habitat shift
• Habitat dependent migration
Mobile (high encounter rate)
Simple sensory system
Use of a single cue
Low
Likelihood
High

fee_2322_f3.tif


Fitness consequences
Low breeding frequency
No parental care
Dispersive offspring
Long-lived
Mobile
Difficult to tag/mark
High breeding frequency
Parental care
Non-dispersive offspring
Short-lived
Sessile
Easy to tag/mark
Habitat selection
Habitat transition not observable
Habitat transition infrequent
Movement cannot be logged in the field
Not suitable for lab testing
Habitat cues unknown
Habitat transition observable
Habitat transition frequent
Movement can be logged in the field
Suitable for lab testing
Habitat cues known
Low
Feasibility
High

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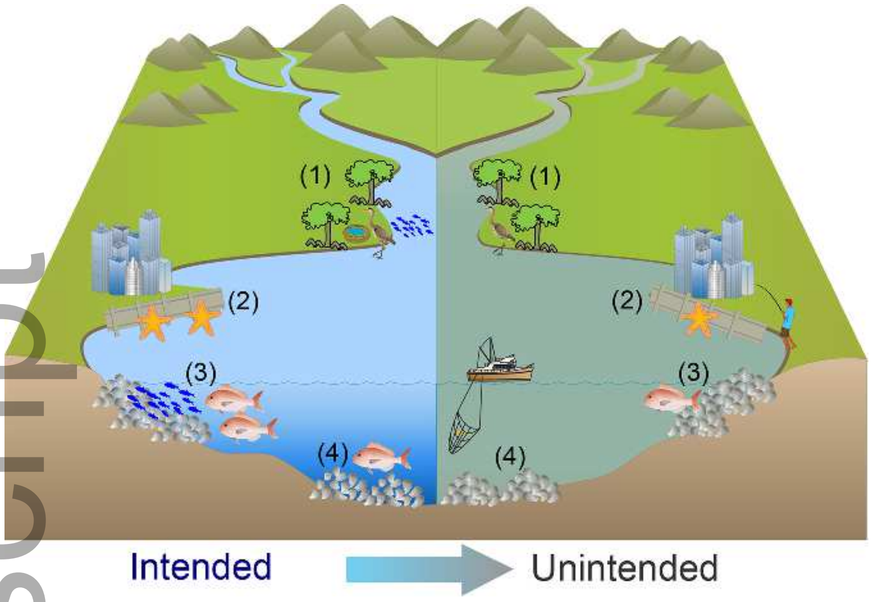
(1)
(1)
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(4)
(4)
Intended
Unintended

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