Artificial light at night is globally widespread (Cinzano et al. 2001), rapidly expanding in spatial extent (Hölker et al. 2010), and shifting in its spectral characteristics (Davies et al. 2013a). Increasing concern over these trends has recently fuelled a surge in research toward understanding the ecological impacts of artificial light pollution (eg Davies et al. 2012, 2013a; Stone et al. 2012; Dominoni et al. 2013). While the impacts of light pollution are increasingly well documented in terrestrial ecosystems, marine habitats have received comparatively little attention (Depledge et al. 2010). Indeed, in a recent survey in which 592 coastal scientists were asked to prioritize global coastal research questions, artificial light was not included (Rudd and Lawton 2013). Yet, worldwide, more than a billion people (~23% of the global population) live within 100 km of a coastline (Small and Nicholls 2003), and many coastal marine ecosystems are exposed to artificial light at night. Here, we draw attention to artificial light as an environmental issue in marine systems, document its current spatial extent, and highlight a wide array of known and potential ecological impacts.

In a nutshell:

- Artificial light pollution is globally widespread in marine environments, altering the natural colors, cycles, and intensities of nighttime light, each of which guide a variety of biological processes.
- Known and potential impacts include those on navigation, reproduction and recruitment, predator–prey interactions, and communication in a myriad of marine species and ecosystems, including some of the world’s most biologically diverse and functionally important.
- Research into these impacts is needed to inform conservation strategies and policy decisions relevant to the holistic management of marine ecosystems experiencing an increasingly diverse array of anthropogenic stressors.

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Satellite images of the Earth’s nighttime lights are a testimony to humankind’s widespread colonization and subsequent influence on the planet’s ecosystems (Figure 1). As an initial estimate, in 2010, 354,760 km (22.2%) of the world’s coastlines (excluding Antarctica) were exposed to nightly artificial light pollution (see Table 1 for details). While it might be expected that the coastlines of the developed world are most affected, this is not so: Asia and Africa, for example, have the second and third highest percentage of coastline influenced by light pollution, respectively, with Europe having the highest (Figure 1; Table 1). The amount of artificial light on land is continuing to increase at a rate of 6% per year globally (Hölker et al. 2010). Given the rapid growth of many developing world economies, future increases are expected to be greater in these regions as compared with the developed world over the coming decades, with unknown consequences for some of the planet’s most biodiverse marine ecosystems (Aubrecht et al. 2008).

Sources of artificial light in the marine environment vary, with shipping and light fisheries contributing as temporary sources in nearshore and offshore waters (Figure 2, a and f). Offshore oil platforms and land-based developments such as towns, cities, and their harbors provide more permanent sources that can increase nighttime light intensities across large geographical areas such as estuaries, bays, and continental shelf seas (Figure 2, b and e). Scattering of upwardly emitted or reflected artificial light in the atmosphere and reflection by clouds (artificial skyglow) further extends the spatial influence of land-based light sources (Kyba et al. 2011) into offshore waters,
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and masks natural rhythms of lunar light intensity (Davies et al. 2013b) that provide information for regulating a number of biological processes in the ocean (Naylor 1999). Ongoing shifts in prevailing technologies are resulting in an increasing use of “white” or broader spectrum lights (Gaston et al. 2012), and a greater variety of spectrally distinct lighting types is creating complex spatial patterns of color and brightness across marine lightscapes at night (Figure 2c), which were previously lit only by the comparatively constant broad spectrum of moonlight (Figure 2d). This is particularly pertinent to depth-dependent biological processes that can be guided by the spectrum of light as it changes through the water column. Blue artificial light will penetrate deeper in the open ocean due to the faster attenuation of red light, increasing its potential scale of influence. Higher concentrations of biological and nonbiological particulates alter this attenuation so that, for instance, green artificial lights would penetrate deepest in temperate regions where phytoplankton absorb other wavelengths.

Given the increasing proportion of coastlines that are artificially illuminated and the variety of ways this alters the natural light regimes with which marine organisms have evolved, it is essential that scientists gain a better understanding of the known and potential ecological consequences of artificial light in marine ecosystems.

**Ecological implications**

The vast majority of species have evolved under natural and predictable regimes of moonlight, sunlight, and starlight. These regimes define species’ activity times (eg nocturnal, crepuscular, diurnal), offer a useful navigational aid, help to regulate and coordinate maturation and reproductive events, and provide a relatively constant irradiance spectrum that can regulate physiology and inform visually guided behaviors such as predation and communication (Gaston et al. 2013). Many of these processes are affected by artificial nighttime light in terrestrial ecosystems: for example, in birds, sexual maturation is advanced (Dominoni et al. 2013), foraging effort is intensified (Titulaer et al. 2012), and the timing of dawn song is extended into the night (Nordt and Klenke 2013). Some species are attracted to artificially lit areas where they may experience increased predation (Rydell 1992), while others avoid artificially lit areas (Stone et al. 2012), and so are displaced from habitats that would otherwise be suitably dark in the absence of artificial lighting. Many of the same types of light cues are just as intrinsic to the ecology of marine species as they are for terrestrial species. Artificial nighttime light is therefore likely to affect a diverse array of ecological processes in the marine environment (Figure 3). Here, we highlight some of the major impacts, providing examples

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Table 1. The spatial extent of coastal light pollution

<table>
<thead>
<tr>
<th>Region</th>
<th>Kilometers of coastline affected</th>
<th>Percent of coastline affected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Europe</td>
<td>115,383</td>
<td>54.3</td>
</tr>
<tr>
<td>Asia (excluding Russia)</td>
<td>113,166</td>
<td>34.2</td>
</tr>
<tr>
<td>Africa</td>
<td>18,589</td>
<td>22.1</td>
</tr>
<tr>
<td>South America</td>
<td>24,197</td>
<td>15.5</td>
</tr>
<tr>
<td>North America</td>
<td>64,356</td>
<td>11.8</td>
</tr>
<tr>
<td>Oceania</td>
<td>11,692</td>
<td>7.9</td>
</tr>
<tr>
<td>Russia</td>
<td>7,377</td>
<td>6.1</td>
</tr>
<tr>
<td>Total</td>
<td>354,760</td>
<td>22.2</td>
</tr>
</tbody>
</table>

Notes: Values are derived from a Behrmann equal-area projected Defense Meteorological Satellite Program Operational Line Scan nighttime lights image from 2010 (see Figure 1). Light-polluted areas of coastline were defined as those where the pixel intensity was greater than five on an uncalibrated scale between zero and 63. Antarctica was omitted when calculating the total % of coastline.

Figure 1. The global extent of marine light pollution. Images are derived from the Defense Meteorological Satellite Program Operational Line Scan nighttime lights image for 2010 (Behrmann equal-area projected; pixels aggregated to 8-km resolution). Graph inserts in (a) represent the distribution of artificial light intensity across continental coastlines, calculated from raw data at the original ~800-m resolution. The x axes represent artificial light intensity (0–63 Digital Number [DN]), where the brightest pixels are assigned the highest values; the y axes represent log km of coastline affected by that intensity of light. Coastlines (highlighted) were defined as anywhere up to 10-km inland.
from taxa known to be affected as well as functionally important taxa that are likely to be affected.

Orientation

Perhaps the best-known impact of artificial light is the disorientation experienced by species that use natural light cues to navigate, most notably birds and sea turtles (Tuxbury and Salmon 2005; Merkel 2010) in marine systems. Bird strikes, involving a variety of species, on artificially lit vessels at sea are common at night (Merkel 2010), whereas coastal lighting disorients turtle hatchlings and prevents or delays them from locating the sea (Tuxbury and Salmon 2005), ultimately reducing the number of turtle nesting sites in artificially lit locations (Mazor et al. 2013).

In the intertidal environment, moonlight provides a compass for navigation by the invertebrate sandhopper Talitrus saltator (Ugolini et al. 2005), raising the question of whether artificial lighting is disrupting lunar-orientated tidal migrations. This behavior is also seen in terrestrial species, such as dung beetles (Dacke et al. 2003), and is likely to be widespread across both terrestrial and marine arthropods. Behavioral responses to artificial light have also been demonstrated in various fish species (Marchesan et al. 2005). For instance, sea cages that are artificially lit affect depth selection in Atlantic salmon (Salmo salar; Oppedal et al. 2011), while coastal lighting around estuaries can aggregate fish in artificially lit habitats (Becker et al. 2012). Indeed, the attraction of the larval stages of many fish species to artificial lights has led to the development of light-based trapping methods that are analogous to those used for trapping nocturnal Lepidoptera (Doherty 1987). Artificial lights are commonly used by the fishing industry to attract and catch several squid species. Those lights are so powerful that nighttime satellite images can be used to quantify fishing pressure, spawning grounds, and migration routes (Figure 2f; Kiyofuji and Saitoh 2004). The geographically widespread use of powerful artificial lights in these fisheries is likely to influence the behavior and survivorship of many nontarget as well as target species over large spatial scales.

Light intensity and spectra are especially useful cues by which organisms regulate their depth in the pelagic environment where landmarks are absent. While some species have evolved the ability to navigate horizontally via detection of the Earth's geomagnetic field, the visible portion of the electromagnetic spectrum is one of the most important means of vertical navigation. Consequently, light intensity informs the vertical movement of zooplankton species that migrate to surface waters at night to graze while avoiding predation (Cohen and Forward 2009). Given that artificial skyglow is more widespread than direct artificial light (Cinzano et al. 2001) and frequently occurs at intensities greater than (and thus directly interferes with) natural lunar sky
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brightness (Davies et al. 2013b), it seems likely that temporal patterns of zooplankton migration will be affected in artificially lit waters. Indeed, artificial light reflected back to Earth from urban areas (a primary source of artificial skyglow) limits the vertical migration of Daphnia spp in freshwater lakes (Moore et al. 2000).

The nightly vertical movement of zooplankton toward the ocean surface is arguably the largest daily migration of biomass on the planet (Hays 2003). The consumption of near-surface phytoplankton by migrating zooplankton during the night and the subsequent defecation of fecal pellets at depth during the day (Hays 2003; Cohen and Forward 2009) constitutes a major pathway in the carbon cycle, and the adaptive behavior of predators to the vertical movements of their prey results in the daily migration of entire food webs (Hays 2003). Artificial light pollution has the potential to disrupt this vertical migration pattern, and with it the productivity and cycling of carbon and nutrients in marine ecosystems.

Reproduction and recruitment

The movements of the celestial bodies create predictable regimes in the intensity and duration of light that organisms use as a clock to synchronize activity (Naylor 1999). In the marine environment, many species use natural light regimes to regulate rates of reproductive maturation and synchronize broadcast spawning events (the release of male and female gametes into the surrounding environment). In the aquaculture industry, these photoperiodic responses are manipulated with artificial lighting to control sexual maturation (Oppedal et al. 2011). A classic example of apparent lunar periodicity in broadcast spawning is the palolo worm (Eunice viridis), which releases gametes over a few days of the year during the third-quarter moon in October (Naylor 1999). Other marine polychaetes apparently also synchronize reproductive events to lunar cycles (Bentley et al. 1999), as do some corals (Harrison 2011) and echinoderms (Lessios 1991). The degree to which lunar light intensity alone regulates such events, as compared to the role of variables such as day length, temperature, and tidal conditions, is unknown for many taxa. However, it seems likely that in numerous cases a combination of these cues is used to regulate gamete development, with lunar light intensity providing the final trigger for spawning (Harrison 2011). In addition, it has been postulated that the spectral contrasts between moonlight and daylight vary more predictably than intensity alone (Sweeney et al. 2011), implying that changes in artificial light spectra, and consequently the colors of skyglow, may also affect broadcast spawning synchronicity. The advantage of synchronizing spawning events is unclear, although it is probably linked to maximizing reproductive contact between conspecifics (Harrison 2011). Lunar light intensity and day length offer two cues that vary predictably and independently of other environmental variables that are influenced by more stochastic Earth-bound processes. This includes tidal height and current velocity, which – in contrast to the single detectable peak of lunar brightness every 29.5 days – have multiple peaks within this time frame that are more spatially variable in magnitude and timing. The “lunar clock” can, however, be masked by artificial skyglow (Davies et al. 2013b), which may interfere with the synchronization of spawning events, resulting in decreased cross fertilization and ultimately a decline in recruitment among broadcast-spawning species.

It is well known that the intensity and spectral characteristics of light inform the orientation and settlement of the larvae of a broad array of sessile invertebrates (Thorson 1964), including corals, arthropods, polychaetes, echinoderms, tunicates, and bryozoans. Altering the intensity or spectral signature of light could interfere
with both the pelagic and pre-settlement stages of marine invertebrate life cycles, with major consequences for sessile invertebrate ecosystems. For example, as in many shallow seabed communities, coral reef assemblages are structured vertically with increasing depth (Vermeij and Bak 2002). Coral larvae identify their optimum settlement zones using the intensity and spectral characteristics of light (Mundy and Babcock 1998), which vary with depth due to the differential absorption of different wavelengths of light in water. In a similar fashion, light intensities allow the larvae of sessile invertebrates in shallow subtidal environments to avoid settling in areas that are sufficiently lit to facilitate the growth of competitive algal species (Glasby 1999), giving rise to horizontal structuring of ecological communities. Artificial lights alter the spectrum and intensity of light that larvae experience, resulting in suboptimal selection of sites to settle and metamorphose into adult form. For instance, barnacle larvae can choose settlement zones under white light intensities of $1 \times 10^5$ lumen m$^{-2}$ (lux) (Crisp and Ritz 1973), which is four orders of magnitude less than that emitted by urban skylow (Gaston et al. 2013). In sessile invertebrates, settlement site selection ultimately decides survival and reproductive success; hence changing natural light regimes could plausibly affect the composition and functioning of these communities, the members of many of which (eg reefs) are ecosystem engineers.

**Predation**

A variety of cryptic anti-predator defenses have evolved in the marine environment, of which camouflage and nocturnality are two of the most widespread. The ability to locate prey or avoid a predator depends largely on the predator’s ability to recognize its quarry against complex backgrounds of shape, color, and pattern, and the prey’s ability to disguise itself to avoid detection (Troschianko et al. 2009). Many species have evolved color patterns to blend in with their environment and nocturnal behaviors to avoid predator contact, while polymorphic color varieties allow some species populations to rapidly adapt to different environments and to predators with contrasting methods of prey search behavior. The increased intensity of artificial light as compared to moonlight, and the broadening of artificial light spectra, provides greater opportunities for predatory species to recognize their prey, potentially allowing diurnal and crepuscular foraging behaviors to encroach further into the night, displacing nocturnal prey or predator species from habitats that were previously exposed only to natural regimes of darkness. Prey species may experience intensified predation pressure, resulting in localized population declines or shifts in the frequency of particular polymorphs toward types that are less conspicuous under artificial night lighting.

Several studies have shown that the attraction of nocturnal Lepidoptera to street lights at night results in aggregations upon which opportunistic bat species often prey (Rydell 1992). In the marine environment, direct artificial light aggregates both small prey fish and larger predatory species, increasing predation pressure in a similar fashion (Becker et al. 2012). In another example, turning off the lighting on bridges spanning the Puntledge River in British Columbia, Canada, reduced the intensity of predation by harbor seals (*Phoca vitulina*) on migrating juvenile Pacific salmon (*Oncorhynchus* spp; Yurk and Trites 2000). Similarly, artificially lit intertidal mud flats allow coastal waders to employ more profitable visually guided foraging behaviors later into the night (Dwyer et al. 2013). Where the distribution of artificial light is patchy, this can result in competition for optimal foraging zones based on artificial light intensity (Dwyer et al. 2013) and intensified predation within more brightly lit patches.

Many marine taxa emit light generated from biochemical reactions (bioluminescence; Figure 4) to avoid predation or to lure prey. Although popular perceptions of bioluminescence are often associated with the deep sea, it is evolutionarily and geographically more widespread throughout the oceans, occurring in fish, tunicates, echinoderms, arthropods, annelids, ribbon worms (Nemertea), cnidarians, mollusks, dinoflagellates, bacteria, and chaetognaths in both oceanic and nearshore environments (Haddock et al. 2010). Anti-predator strategies include using light displays to confuse predators, sacrificing light-emitting body parts to distract predators, attracting the predator’s own predators, and mimicking ambient light from above to avoid silhouette detection by predators from below (Haddock et al. 2010). The effects of artificial lighting on these types of interactions are thus far largely unexplored. The narrow spectrum of 590-nanometer (nm) visible light emitted by widely used 20th-century low-pressure sodium lighting technologies and the short-wave spectral peak of ~470 nm emitted by most bioluminescent marine taxa (Haddock et al. 2010) suggest that in the past, in nearshore environments at least, land-based municipal lighting may have had limited impacts on interactions governed by bioluminescent communication. However, the increasing use of broader spectrum lighting technologies (eg light-emitting diodes [LEDs]) over the coming decades will result in an increasing amount of land-based artificial light illuminating the 470-nm communication channel (Davies et al. 2013a) in inshore waters.

**Figure 4.** The bioluminescent comb jelly, *Beroe cucumis*, occurs at depths that can be penetrated by artificial light.
Complex eyes have evolved independently in several marine lineages, including fish, cephalopods, and arthropods, and just as in many terrestrial taxa, the spectra, patterns, and angles of light reflected from individuals are useful elements in inter- and intraspecies communication. As with butterflies and birds, the boldness of colorful markings communicates competitive fitness to potential mates in many marine arthropods (Detto 2007) and fish (Siebeck et al. 2010). Cephalopods use adaptive displays of color and pattern, created by a combination of reflecting and color-changing cells to communicate (Mäthger et al. 2009); the iridescent markings on squid, for example, vary in appearance depending on the position of the onlooker. This could facilitate communication of shoaling behavior between conspecifics, a type of visual communication that may also be exploited by fish for the same purpose (Mäthger et al. 2009).

The current introduction of artificial lights that emit broader spectra means that visually guided behaviors such as mate selection are more likely to be influenced by light pollution, since many of the physical features that are used to communicate fitness will be more recognizable under whiter lighting (Davies et al. 2013a). This includes the use of lights that emit ultraviolet (UV), a communication channel that some species exploit almost exclusively to avoid predation or to distinguish between closely related species (Siebeck et al. 2010). The Ambon damselfish (*Pomacentrus amboinensis*), for instance, uses UV light reflected in species-specific patterns to discriminate between conspecifics and other species of damselfish that appear identical at visible wavelengths (Siebeck et al. 2010).

Bioluminescence signals are also used in sexual communication by marine species in a way that is analogous to fireflies (Haddock et al. 2010). Examples include ostracods that attract mates using bioluminescent signals and ponyfishes (*Leiognathidae*) that use dimorphic bioluminescent displays to differentiate between sexes (Haddock et al. 2010). The potential for artificial lights to disrupt mating behaviors that rely on bioluminescent cues has been raised with fireflies (Longcore and Rich 2004); artificial light could also possibly disrupt such interactions in marine taxa.

**Moving forward**

We have drawn attention to artificial light as a threat to marine biodiversity and highlighted some of the diverse array of species, behaviors, interactions, and ecosystems that are likely to be affected. The challenge now is to quantify the extent of the threat posed in regions where such species and ecosystems exist, to develop a sound knowledge base from which to design protective measures, and to identify how such measures can best be implemented. In this section, we highlight some of the key components of such work.
predictive models of where future impacts are most likely to occur. Understanding where sensitive species and ecosystems are exposed to artificial light also requires that mapping and modeling take account of vertical as well as horizontal variability in artificial light, so that factors such as turbidity, which determines how spectrum and depth interact to affect intensity, can be quantified.

**Developing a sound knowledge base**

As with many emerging ecological issues, research into marine light pollution will initially focus on documenting the range of species, behaviors, and areas that are affected. It is also imperative that investigators explore the context of these effects to identify ecologically sound mitigation measures that could provide alternatives to the complete elimination of artificial lighting (as this will not always be possible). For example, many biological responses – including those associated with communication, larval recruitment, or phototactic reactions in mobile fauna – are likely to be spectrally dependent. Narrow-band optical filters and LEDs offer the potential for controlling the intensity and spectrum of artificial light independently, enabling investigators to identify those regions of the light spectrum that have minimal biological impacts. Experiments of this nature can be used as a basis for the development of mitigation strategies, while those that document the impacts of artificial lighting in the environment provide the impetus for doing so.

Long-term databases offer opportunities to quantify the role of light pollution in driving population fluctuations, and to monitor the success of preventative and remedial measures. An example of one such monitoring scheme is the British Antarctic Survey’s bird strike log, where bird strikes on ships are digitally recorded. Rolling out such a program across shipping globally would help to identify “hotspots” of human–wildlife conflict, where operational procedures could be put in place to minimize ecological impact. The data generated also offer the capability to identify seasonal and climatic influences on bird strike occurrences, and to evaluate the success of mitigation measures such as switching off deck lighting during non-operational hours and installing lights with narrow emission spectra that reduce bird collision incidents (Secretariat of the Antarctic Treaty 2010; Merkel 2010).

To appreciate the consequences of marine light pollution for the goods and services provided to humanity by marine ecosystems, investigators can focus on whether direct impacts on one species can result in cascading impacts throughout ecological networks. For instance, while there is evidence that artificial light facilitates nocturnal visual foraging in wading birds (Dwyer et al. 2013), it is not known how this affects the macro-infaunal communities on which the birds feed or the ecosystem processes these communities perform. Many of the ecological responses to artificial light discussed here could lead to secondary effects on associated species, trophic structure, and ecosystem functioning, thereby compromising the delivery of ecosystem services. Various long-term ecological field manipulations of light pollution have recently been established in terrestrial systems. By artificially illuminating previously dark habitats at night, these experiments are elucidating the impact of light pollution at the community and ecosystem levels. The intertidal and shallow sublittoral marine environments offer several tractable systems where similar experiments could be performed.

**Reducing environmental impacts**

Initiatives to preserve naturally lit landscapes exist through national and international programs that recognize the value of dark skies (eg www.darkskyparks.org). The International Dark-Sky Association’s Dark Sky Parks program, The Starlight Foundation’s Starlight Reserves, and the UK’s Science and Technology Facilities Council’s Dark Sky Discovery Sites are all examples of initiatives that award dark sky status to areas where light pollution is minimized. By participating in such programs, local governing authorities are incentivized to adopt measures that preserve natural darkness and the cultural, ecological, aesthetic, and scientific benefits this provides. Although coastal regions have been awarded status under some of the national schemes, expanding these initiatives more widely to include “marine dark sky parks” would be a positive step toward protecting currently dark regions of the marine environment against encroaching light pollution, while capitalizing on benefits to society, the environment, and economic gains through nature tourism.

Artificial light pollution has only recently become widely recognized as an environmental issue. Statutory tools for mitigating against its ecological impacts are therefore largely lacking in marine environments. At present, the International Convention for the Prevention of Pollution from Ships (MARPOL) does not recognize artificial light as a pollutant. Some examples of voluntary mitigation measures have, however, been adopted by individual nations in sensitive areas such as the Antarctic, although these guidelines have yet to be adopted formally by all Antarctic Treaty Committee members (Secretariat of the Antarctic Treaty 2010). Indeed, in many cases it is difficult for policy makers to introduce statutory mitigation measures where these conflict with local economic gains or operational safety issues and there is a limited understanding of the severity of the problem. This is highlighted in the European Commission Marine Strategy Framework Directive (Commission decision 2010/477/EU; MFSD 2010). Despite being recognized under Descriptor 11, the Commission did not specify any formal criteria for light, stating that “Additional scientific and technical progress is still required” (MFSD 2010). As a result, standards defining environmentally “acceptable” levels of light pollution in marine waters are unlikely to feature in the corresponding legislative tools drawn up by...
the member nations of the European Union (EU). A concerted research effort is clearly needed to document and understand the environmental impacts of light pollution in the marine environment so that effective statutory protective measures can be developed.

**Conclusion**

Artificial light pollution is a global environmental issue, the ecological impacts of which are only now beginning to be examined in detail. Current knowledge of these impacts in marine ecosystems is insufficient to determine the scale of the problem and its likely interactions with other anthropogenic pressures, nor can it inform the implementation of effective protective measures. Yet artificial light at night is potentially damaging to some of the world's most biologically diverse and functionally important marine ecosystems, and as such should be considered a threat to human well-being. In the absence of sound scientific understanding, precautionary measures should be taken to mitigate the ecological impacts of light pollution in marine environments wherever possible. Where statutory tools are lacking, introducing voluntary codes of practice and seeking incentives to preserve naturally lit areas through dark skies initiatives should be encouraged as preventative measures. A concerted research drive is needed to inform the design of realistic and effective management strategies that can bring benefits to both ecology and society. The scale of this research landscape is extensive and is truly interdisciplinary, demanding input from terrestrial, freshwater, and marine ecologists; physical oceanographers; remote-sensing scientists; and marine engineers.

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