Global change and marine communities: Alien species and climate change

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Abstract

Anthropogenic influences on the biosphere since the advent of the industrial age are increasingly causing global changes. Climatic change and the rising concentration of greenhouse gases in the atmosphere are ranking high in scientific and public agendas, and other components of global change are also frequently addressed, among which are the introductions of non indigenous species (NIS) in biogeographic regions well separated from the donor region, often followed by spectacular invasions. In the marine environment, both climatic change and spread of alien species have been studied extensively; this review is aimed at examining the main responses of ecosystems to climatic change, taking into account the increasing importance of biological invasions.

Some general principles on NIS introductions in the marine environment are recalled, such as the importance of propagule pressure and of development stages during the time course of an invasion. Climatic change is known to affect many ecological properties; it interacts also with NIS in many possible ways. Direct (proximate) effects on individuals and populations of altered physical–chemical conditions are distinguished from indirect effects on emergent properties (species distribution, diversity, and production). Climatically driven changes may affect both local dispersal mechanisms, due to the alteration of current patterns, and competitive interactions between NIS and native species, due to the onset of new thermal optima and/or different carbonate chemistry.

As well as latitudinal range expansions of species correlated with changing temperature conditions, and effects on species richness and the correlated extinction of native species, some invasions may provoke multiple effects which involve overall ecosystem functioning (material flow between trophic groups, primary production, relative extent of organic material decomposition, extent of benthic-pelagic coupling). Some examples are given, including a special mention of the situation of the Mediterranean Sea, where so many species have been introduced recently, and where some have spread in very large quantities.

An increasing effort by marine scientists is required, not only to monitor the state of the environment, but also to help predicting future changes and finding ways to mitigate or manage them.

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1. Introduction

Biological invasions are being recognized as an important element of global change, following the observation of increasingly spectacular developments of alien species in various regions of the world. Climate change and other components of global change such as increasing deposition of nitrogen and pollutants, and habitat disturbance by human activities, can affect species distribution and resource dynamics in both terrestrial and aquatic ecosystems and consequently can interact with biological invasions (Dukes and Mooney, 1999; Vitousek et al., 1997).

The effect of climate change and invasive species have been implicated in the decline and even collapse of several marine ecosystems (Harris and Tyrrell, 2001; Stachowicz et al., 2002; Frank et al., 2005) and are known to affect the presence of pathogens (see Drake et al., this issue). When many stressors act in synergism they may eventually have unexpected and irreversible consequences for the native communities and also may impact economically valuable human activities such as fisheries in a particular region (Occhipinti-Ambrogi and Savini, 2003; Whitfield et al., 2007). This scenario implies a direct economic cost...
within marine environments that is related to introduced species, a cost that is just beginning to be recognized (Pimentel et al., 2000).

Impact of invasive species has been defined by Parker et al. (1999), who also discussed, from empirical examples and theoretical reasoning, a variety of measures of impact. In the marine environment, Ruiz et al. (1999) describe impact by alien species and interactions with other stress factors. Stressing the importance of this man-induced disturbance, Elliot (2003) observes that there are many aspects in which introduced marine organisms can be regarded as being no different from chemical pollutants and encourages the use of the term biological pollution.

On the other hand, beneficial aspects of introductions are claimed, since intentionally introduced species have significantly contributed to aquaculture production (FAO DIAS, 1998), as well as fisheries and angling (Minchin and Rosenthal, 2002). Unintentionally introduced species, such as the Erythrean species which entered the Mediterranean Sea, have become locally of commercial importance (Golani and Ben Tuvia, 1995); the Mediterranean mussel Mytilus galloprovincialis, accidentally introduced to the West coast of South Africa in the mid 1970s, was deliberately introduced to the South coast for mariculture purposes, despite the fact that it had become invasive, outcompeting local mussels (Branch and Steffani, 2004).

Ecological principles for predicting the success of invasions in new environments have always been highly debated, yet have profound implications for management and control of human-mediated introductions. At the same time, predicting the effects of climate change on invasions is more difficult, because ecologists must face a complicated pattern of perturbations, independently affecting species and ecosystems.

Dukes and Mooney (1999) stated that the emergent pattern of predictions on the effect of global change on invasions leads us to expect that invasive alien species could be favoured, so that the impacts of invasions on ecosystems would be exacerbated. In this review some general principles of invasions in the marine environment and some general principles of various elements of global climate change will be recalled, in order to help the interpretation of phenomena observed in different seas. Special reference is made to the Mediterranean Sea, which is one of the most affected seas of the world in this respect, both in terms of length of time that invasives have been present and in numbers of alien species detected (see Galil, this issue).

2. Biological invasions in the sea

The establishment of NIS in new ecosystems has been the subject of the so-called “invasion ecology” that has frequently concentrated on the identification of “invasiveness” characteristics of species that proliferate in novel habitats (Gray, 1986; Lodge, 1993; Williamson, 1996; Kolar and Lodge, 2001) and/or “invasibility” characteristics of particular habitats that are susceptible to the proliferation of NIS (Wolff, 1999; Shea and Chesson, 2002; Nehring, 2006).

The role of propagule pressure (i.e. the number of individuals introduced and the number of introduction attempts) is obviously very important in determining the success of NIS establishment, although it is not always taken into account in studies on biological invasions (Williamson, 1996; Ruiz et al., 2000; Ruesink, 2005; Colautti et al., 2006). In the marine environment, propagule pressure has increased steadily from NIS transport via ships (Carlton, 1985; Hewitt, 2002; Coutts et al., 2003) and via aquaculture (Casal, 2006), along with a range of other activities (Minchin, this issue) such as the opening of navigable canals (Por, 1978; Galil, 2000) and the trade of species for aquaria (Semmens et al., 2004; Calado and Chapman, 2006; Bolton and Graham, 2006).

Propagule pressure is not easily measurable directly, except with intentional species introductions (e.g. transplanting of molluscs or release of commercially important fishes and crustaceans), but can be related with some measure to the intensity of unintentional introductions, such as the estimated quantities of discharged ballast waters, or number of boats and ships that might carry fouling on hulls, or the presence of oyster and mussel cultures that can favour hitch-hiking species epibionts, or parasites of imported molluscs.

Given that NIS are introduced non-randomly through these vectors, failing to consider propagule pressure causes a bias in the interpretation of observed results. Both for invasiveness and invasibility, the characteristics of good invaders and susceptible habitats can be confounded by propagule bias (Colautti et al., 2006). Although the lack of knowledge about dose-response relationships between propagule supply and invasion success represents a critical gap for invasion science, management actions to reduce transfers must proceed concurrently with scientific efforts to evaluate dose-response and efficacy (Ruiz and Carlton, 2003; Lockwood et al., 2005).

So, when we consider the impact of global change, we first of all take into account the magnitude of release of NIS propagules, and secondly the effects of climatic change. Wonham and Carlton (2005) have discussed the literature data of the Northeast Pacific Coast (Northern California to British Columbia) giving indications of the port traffic and of oyster culture that were in accord with the observed spatial and temporal pattern of NIS introduction. In European waters some figures have been published by Stretaris et al. (2005) and Gollasch (2006). The latter author estimates that in European coastal waters 39% of the observed NIS were transported by ships (22% in ballast waters and 17% as hull fouling), 16% by aquaculture, 9% were intentionally released, and 24.5% entered through the Suez canal.

Development of NIS populations is a dynamic process involving different stages (Colautti and MacIsaac, 2004) (Fig. 1). Potential invaders begin their life history as prop-
agules residing in a donor region (stage 0), like the port of call of a ship pumping ballast water or the site of production of bivalve seed shipped for aquaculture. They subsequently pass through a series of filters that may preclude transition to subsequent stages. Stage 1 corresponds to the uptake of propagules by the transport vector. After passing through a survival and release filter, stage 2 is reached, corresponding to some individuals settled in the new environment (e.g. metamorphosed larvae in the port where the ship has deballasted or individuals that have escaped to the wild from aquaculture facilities).

The passage through the environment survival and reproduction filter leads to the establishment of a NIS population (stage 3). The success of the NIS after establishment is governed by two different filters: a “local dispersal filter”, mainly connected to propagule pressure, determines which stage 3 species reaches stage 4a (widespread) or which stage 4b species (dominant) can reach stage 5 (widespread and dominant). The environmental and community suitability filter acts regulating the passage from stage 3 to stage 4b and from stage 4a and stage 5.

Fig. 1. Stages in the development of an invasive non indigenous species. Transition between stages involves the passing of propagules through filters. The success in reaching a new stage is determined, besides propagule pressure, by two broad categories of factors: physical–chemical matching and biotic resistance or facilitation. The determinants may act in a positive (+) or negative (−) way. Modified from Colautti et al. (2006).

As an example, most of the more notorious invaders (e.g. the Manila clam, *Ruditapes philippinarum*) form stage 5 populations because they have been introduced repeatedly to ideal habitats, offering niche opportunities. Such stage 5 species have therefore passed through both the “local dispersal” and “environmental survival and reproduction” filters. On the contrary, other species became widespread (stage 4a), yet they rarely achieved high densities along the coasts of the Mediterranean, like the algae *Asparagopsis armata* and *Lophocladia lallemandi* (Ribera Siguan, 2002), which have been repeatedly introduced. These two examples illustrate the importance of the propagule pressure determinant, compared with determinants related to biotic and physical–chemical conditions.

Verlaque and Boudouresque (2004) did not find any connection between the numerous (105) species of introduced algae and water warming in the Mediterranean, and most such introductions are better explained by the presence of intense aquaculture in the hotspots of alien species.

Finally the introduction of the decapod crustacean *Dyspanopeus sayi* in the Northern Adriatic may be an example of stage 4b population. After their introduction in the Lagoon of Venice in 1992 (Froglia and Speranza, 1993), it reached high abundances locally (Mizzan, 1995; Mistri, 2004), then declined and is now rather rare (Mistri and Mizzan, personal communications).

Climatic change is known to affect many ecological properties (Walther et al., 2002); it interacts also with NIS (whose propagule pressure is increasing steadily), directly by altering physical–chemical conditions (primarily temperature but also related oceanographic characteristics), and indirectly contributing to the change in the new communities patterns.

### 3. Impact of climatic change on marine organisms (proximate effects)

Anthropogenically induced global climate change has profound implications for marine ecosystems, well beyond the direct influence of temperature on marine organisms. Both abiotic changes and biological responses in the marine environment are complex and deserve a great deal of research in order to interpret actual patterns and to predict future changes (Harley et al., 2006).

Following the scheme by Harley et al. (2006) in Fig. 2, changes in the life cycle of a generic marine species affected by abiotic environmental changes will be considered first. These include effects on dispersal and recruitment and on individual performance.

Climate varies naturally across a range of temporal scales including seasonal cycles, inter-annual patterns such as the El Nino Southern Oscillation (ENSO), inter-decadal cycles such as the North Atlantic Decadal oscillation, and multimillennial-scale changes such as glacial to inter-glacial transitions. This natural variability is reflected in evolutionary adaptations of species and biogeography. In the Mediterranean Sea, for instance, a surface temperature increase of about 1 °C in the period 1974–2004 has been reported by Salat and Pascual (2002). In deep waters, a 0.12 °C increase is estimated for the last 40 years (Béthoux et al., 1990; Béthoux and Gentili, 1996; Goffart et al., 2002).

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**Fig. 2. Main response pathways of ecological systems to global climatic change. Modified from Harley et al. (2006).**
The effects of warming climate are primarily a cause for physiological stress, which acts more strongly on species already near their tolerance limit (Laubier, 2001). Anomalous temperature stress can cause mass mortalities in benthic organisms (Cerrano et al., 2000; Pérez et al., 2000; Garrabou et al., 2001) that result in empty niches for new colonisers. However, the responses of the organisms are often very subtle and cannot be assessed simply by exposing different life stages to a range of temperatures. In particular, in seasonal environments where conditions change predictably, each species may have a temporal or seasonal niche, caused for instance by differences in growth rate, patterns of mortality, timing, duration and magnitude of reproductive output.

Stachowicz et al. (2002) demonstrated temporal complementarity in recruitment for dominant invertebrate species on hard bottoms, noting that the recruitment pattern of the NIS Botryllloides violaceus coincided with a period of low recruitment of other native species of ascidians (Fig. 3). The competition for open space on the substrate is heavily influenced by the timing of recruitment, and this in turn is highly dependent on temperature. Changing seasonal patterns of temperature may favour the settlement of invasive species in a particular time of the year, and with long lasting consequences in preventing the recruitment of native species later. The consequences of temperature change also include vertical stability of the water column and upwelling. Changes in atmospheric circulation might also change storm frequency and precipitation patterns and alter circulation (Astraldi et al., 1995), and hence the dispersion routes of introduced species.

Together, increases in global mean temperatures and elevated CO₂ will result in a cascade of physical and chemical changes in marine systems. While the concentration of CO₂ has reached 378 ppm (and other greenhouse gases have also increased dramatically), global air and sea surface temperatures have risen in the past century by 0.4–0.8 °C (IPCC, 2001). Continued uptake of atmospheric CO₂ is expected to substantially decrease oceanic pH, through an increase of surface-water dissolved inorganic carbon (DIC) and a decrease of carbonate ion concentration. The dissolution of marine biogenic carbonates neutralizes anthropogenic CO₂ and adds to total alkalinity. The extent of dissolution increases as a function of the decrease of calcium carbonate saturation state and recent analyses have shown that much of the CaCO₃ exported out of the surface ocean dissolves in much higher horizons than previously thought. Also, the saturation horizons of aragonite, calcite and other minerals essential to calcifying organisms are changing in several areas of the world oceans. It has been shown that the calcification rate of almost all organisms decreases in response to a decreased CaCO₃ saturation even when the saturation level is more than one. In particular, aragonite producers (including reef building corals) and magnesian calcite producers (like coralline algae) are expected to be more sensitive to changes in saturation (Kleypas et al., 1999; Riebesell et al., 2000; Feely et al., 2004).

In conclusion, climatic driven changes may affect both local dispersal mechanisms, due to the alteration of current patterns, and competitive interactions between NIS and native species, due to the onset of new thermal optima and/or different carbonate chemistry. The magnitude and variety of climatically forced changes in the physical environment will provoke responses in the biosphere thus altering the balance of native species vs. NIS, via changes in population size and effect of interacting species.

The effects of climatic change described above ("proximate effects"), thus lead to "emergent" patterns such as changes in species distributions, biodiversity, productivity and microevolutionary processes (Harley et al., 2006), that are concomitant with the effects of the introduction of NIS, especially if they reach stage 4b or 5 (dominant).

4. Impact of global change on marine ecosystems (emergent properties)

The range expansion of populations of NIS following climatic changes in their new environment has been proposed as an explanation of the increasing rate of successful invasions. As said before, only in a few cases has the corresponding change in propagule pressure been taken into...
account, but evidences of changes in the geographic distribution of NIS are increasingly accompanied by observations of warming in particular areas of the sea.

As far as the Mediterranean Sea is concerned, climate change has been suggested as being particularly important in the establishment of alien species of plants (Gritti et al., 2006) and the development of microalgae e.g. species of Asterodinium (a Dinophyceans genus typical of warm waters) (Gomez and Claustre, 2003). Recently (summer 2005 and 2006) another introduced Dinophyceans, Ostreopsis armata, bloomed repeatedly in the Ligurian sea causing respiratory diseases to tourists in several occasions. Climate change has also been suggested for the expansion of the biogeographical range of benthiic and nektobenthiic marine species, as recorded in the last decade in the western Mediterranean (Francour et al., 1994; Vacchi et al., 1999; Bianchi and Morri, 2000; Laubier et al., 2004) as well as in other areas (Bianchi, 1997).

Erythrean species (of warm water affinity), established in different phases after the opening of the Suez canal, have caused changes in the Levantine part of the Mediterranean far beyond recorded impacts in other marine ecosystems. Nearly half of the fish catches along the Israeli coast consist of Erythrean species (Goren and Galil, 2005). By the 1950s the sudden increase in the populations of Saurida undosquamis, U. moluccensis was attributed to a rise of 1.0–1.5 °C in sea temperature during the winter months of 1955 (see Galil, this issue). The process has accelerated in recent years, with increasing records of newly discovered Erythrean species and expansion towards other areas of the Eastern (Galil and Zenetos, 2002) and Western Mediterranean (Harmelin-Vivien et al., 2005; CIESM, 2005).

While the range expansion of species correlated with changing temperature conditions has been observed in many cases, this has been rarely subjected to testing hypotheses explaining this pattern. For instance, Bachelet et al. (2004) have studied the population of the gastropod Cyclope neritea, known from the Mediterranean and southern Atlantic coasts of the Iberian peninsula, and which recently became established in the French coast of the Bay of Biscayne. They considered the origin of the population, using molecular genetic analyses, and the authors concluded that multiple introductions had occurred (probably with shipment of oysters from Portugal and the Mediterranean). Also, they studied the competition for food resources of C. neritea with the overlapping native gastropod Nassarius reticulatus by laboratory experiments, demonstrating a superior ability of the introduced species to search for and consume carrion. Further Nassarius reticulatus was more subject to digenean trematode parasites.

One of the most debated questions in invasion ecology has been the relative importance of biotic processes (e.g. competition and facilitation) of the native-invader relationship and of the abundance of resources in the invaded habitat. This debate has often postulated that a high resident diversity implied a reduced success in the establishment of NIS (Kennedy et al., 2002).

Stachowicz and Byrnes (2006) provide an illuminating hypothesis on the interplay of native diversity and resource availability (free space available for colonisation on the substratum), analysing the outcome of introduced species establishment on hard bottoms using a wide array of experimental and observational studies. As described before, the success of a particular invader depends not only on its propagule pressure but also on the seasonal timing of the recruitment: at high levels of open space there was a strong positive relationship between native and invader richness. The reduced invader diversity where there was plenty of open space was likely due to non-selective disturbance agents; these affect native and invader diversity in a similar negative manner, resulting in native and invader richness covarying positively as a reflection of extrinsic factors (for instance climate).

When resources were limiting (low space availability) experimental results showed a negative slope in the relationship between native and invader diversity, but in field observations, the data instead showed a flat relationship. As diversity increased, temporal complementarity among species may have increased the consistency of space occupation and decreased the likelihood of invader establishment. The complementarity could have simply balanced out the effects of extrinsic factors, however, the authors observed that effects of biotic resistance were offset by the presence of species (facilitators) that provided secondary substrate on their shells, thus increasing the surface area available for colonisation. In summary, an explanation of the effects of native richness of species on invader richness, is proposed (Table 1 in Stachowicz and Byrnes, 2006), that takes into account availability of resources, biotic interactions and extrinsic factors, among which many could be explained by climatic change. It would be interesting to test the hypothesis on different assemblages, where the limiting factors could be different, and especially where climatic conditions are severe for at least some stages of the organism life cycle.

The most commonly predicted effect of global ocean warming is a poleward shift in the distributional boundaries of species with an associated replacement of cold water species by warm water species. However, Schiel et al. (2005), on the basis of the study of communities colonizing a rocky coastal habitat influenced by the outfall of a power generating station, rejected this prediction, observing that the responses of the communities to ocean warming were mostly unpredictable and strongly coupled to direct effects of temperature on key taxa and to indirect effects operating through ecological interactions. Such direct BACI (Before After Control Impact) studies are infrequent and probably difficult to repeat, especially in areas much larger than the section of coast affected by local temperature changes, so classic records of shifting biogeographic borders are still useful to assess changes that might be related to temperature changes. For instance it has been suggested that thermal pollution from a power plant in Vladivostok (Russia) can render the outfall basin an inter-
mediate step for the introduction and acclimation of tropical species, such as Balanus amphitrite and Molgula manhattensis, brought by long distance vessels (Zvyagintsev et al., 2004).

While marine biological invasions are known to alter nearshore benthic and pelagic communities and are displacing native species (Carlton, 1989; Carlton and Geller, 1993; Cohen and Carlton, 1998), there is no evidence yet that aliens have caused large-scale extinctions in recipient coastal biota (see Carlton, 1993; Leppäkoski et al., 2002; Wolff, 2000), and more research is needed to clarify this crucial relation (Gurevitch and Padilla, 2004; Clavero and Garcia-Berthou, 2005). It must be underlined that the decline in existing populations of native species can be overlooked and go unnoticed in some cases, due to lack of previous data or insufficient taxonomic difficulties, as was suggested by Geller (1999) for the invasion of Mytilus galloprovincialis in Southern California where it replaced the native M. trossulus.

Besides the effects on species richness and the correlated extinction of native species, some invasions may provoke multiple effects which affect the overall ecosystem functioning, including factors such as material flow between trophic groups, primary production, relative extent of organic material decomposition, and extent of benthic-pelagic coupling. Perhaps the most conspicuous example of severe shifts in ecosystem functioning is the invasion of the American carnivorous comb jelly Mnemiopsis leidyi in the Black and Caspian Seas, which resulted in serious declines in zooplankton and anchovy populations, causing ecosystem-wide cascading effects (Ivanov et al., 2000; Shiganova et al., 2001). For a discussion of this case see Olenin et al. (this issue).

Invasions by parasites caused long lasting or even irreversible consequences (Harvell et al., 2002), as in case of Bonamia ostreae, a disease of the European native oyster Ostrea edulis, which caused severe decline in their populations and, as a consequence, destruction of native oyster bed ecosystems (Wolff and Reise, 2002). Other important changes in biological communities resulting from biological invasions have occurred in estuaries, coastal lagoons or in waters of variable salinity (Cohen and Carlton, 1998; Olenin and Leppäkoski, 1999; Nehring, 2006). Rue-sink et al. (2006) calculated the increase of total primary production in the estuarine site of Willapa Bay (Washington, USA) caused by the introduction of rooted plants (>50%) as well as of total secondary production (250%) due to the introduction of bivalves; they found that environments with empty niches have been colonised by species that play novel roles in the ecosystem, with further implications for habitat, detritus and filtration.

The case of the Lagoon of Venice has been described by Occhipinti-Ambrogi (2000). Recently Pranovi et al. (2006) have assessed the changes in the benthic ecosystem of the lagoon induced by introduction of Ruditapes philippinarum and subsequent clam exploitation. Bartoli et al. (2001) described biogeochemical cycles altered by the farming of R. philippinarum in another lagoon of the Po delta complex.

Most studies assume that invaders affect negatively native biota, while a few others contend that aliens in coastal waters seem to play a beneficial role in ecosystem functioning. At least in the short term, some invasions have resulted in a net gain in the number of species present at the local/regional level (Sax and Gaines, 2003). Some authors observe that NIS may often be complementary to natives in their patterns of resource use (Olenin and Leppäkoski, 1999; Reise et al., 2006). Examples of increase of benthic biomass production and improved filtration activity with beneficial effects include Dreissena polymorpha in the Baltic sea (Daunys et al., 2006) and Ensis americanus along coasts of the North Sea (Armonies and Reise, 1998). A more problematic view of the invasion of bivalves in an ecosystem lacking dominant filter-feeder organisms is expressed by Alpine and Cloern (1992).

Also ‘ecosystem engineers’ (Crooks, 2002; Cuddington and Hastings, 2004) contribute to important changes in invaded ecosystems: large scale changes in the physical structure of key habitats in a water body include spawning grounds, underwater sea grass meadows, and biogenic reefs (see Wallentinus and Nyberg, this issue). Among ecosystem engineers, the invasion of the green algae Caulerpa in the Mediterranean has profound effects both on the habitat and on ecosystem functioning (see Galil, this issue and Olenin et al., this issue). Caulerpa taxifolia originated from aquarium release on the coast of France (Jousson et al., 1998) and has expanded to very large areas of the Ligurian and Tyrrenhian Seas (Meinesz et al., 2001). It has been described as “killer alga” (Meinesz et al., 2002) for its alleged property to cover extensively the substrata where it had been introduced without leaving any other previously established vegetation, and profoundly affecting all the biota. It has been regarded as the winner in the competition with the autochthonous Posidonia oceanica that forms the characteristic Posidonia meadows of the Mediterranean, which is now undergoing a rapid decline. Experimental data and observations in different parts of the Mediterranean have shown that, even if direct competition actually exists, Posidonia meadows are overgrown and replaced by C. taxifolia when they are sparse and in a regression stage, whereas well preserved and dense populations show a fair resistance to the Caulerpa expansion. While a possible climate mediated influence has not been investigated in detail (but see Peirano et al., 2005), it is likely that the diffusion of C. taxifolia has been favoured by some weakening of Posidonia due to pre-existing factors. Another factor that might favour C. taxifolia is its ability to change demographic and life-history traits, as suggested by Wright (2005) who studied populations in the 0 stage (source populations) from the subtropical Morton Bay (Australia) and stage 4b (locally dominant) invasive populations in temperate Southeastern Australia.

The other introduced species is Caulerpa racemosa var. cylindracea (Verlaque et al., 2003), a south-western Austra-
Marine alien species are a component of global change in all marine coastal ecosystems. The impact of these species on native communities has been evaluated in many localities all over the world leading to the concept of biotic pollution. This is especially evident in the Mediterranean Sea. The global climatic change affecting the earth’s atmospheric and oceanic system interacts in many ways with global biogeographic changes arising from marine species translocations. Human activities causing emission of greenhouse gases and transport of species across the oceans are increasing at a steady pace. Moreover, the consequences on climate and ecosystems will last for very long time, even if human activities slow down in the near future. The interactions between the two components of global change are potentially very important and have been studied in detail only recently. A common framework for the study of consequences of climatic changes and CO$_2$ increased concentration in the marine environment, and the study of the dynamics of transport, settlement and invasion of alien species, is necessary to understand the long term consequences for marine ecosystems, their goods and services.

Recent developments of an observational and experimental nature have highlighted the importance of considering propagule pressure as a prerequisite in all studies of biological invasions and have indicated a way to disentangle biotic resistance by resident species and/or facilitation by recent settlers from the effects of abiotic conditions that can match the ecological niche of the introduced species. Among these conditions, rapidly evolving ones are the temperature, as well as changing pH and total alkalinity. In this changing marine landscape, deeper insight is needed not only to monitor the state of the environment but also to predict future changes and to mitigate and manage them.

References


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Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change

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Summary

Many coral reefs worldwide have undergone phase shifts to alternate, degraded assemblages because of the combined effects of overfishing, declining water quality, and the direct and indirect impacts of climate change [1–9]. Here, we experimentally manipulated the density of large herbivorous fishes to test their influence on the resilience of coral assemblages in the aftermath of regional-scale bleaching in 1998, the largest coral mortality event recorded to date. The experiment was undertaken on the Great Barrier Reef, within a no-fishing reserve where coral abundances and diversity had been sharply reduced by bleaching [10]. In control areas, where fishes were abundant, algal abundance remained low, whereas coral cover almost doubled (to 20%) over a 3-year period, primarily because of recruitment of species that had been locally extirpated by bleaching. In contrast, exclusion of large herbivorous fishes caused a dramatic explosion of macroalgae, which suppressed the fecundity, recruitment, and survival of corals. Consequently, management of fish stocks is a key component in preventing phase shifts and managing reef resilience. Importantly, local stewardship of fishing effort is a tractable goal for conservation of reefs, and this local action can also provide some insurance against larger-scale disturbances such as mass bleaching, which are impractical to manage directly.

Results and Discussion

The ecosystem goods and services provided by healthy coral reefs are a key component in the economic, social, and cultural fabric of many tropical maritime countries [1, 9]. Until recently, land-based pollution and overfishing were considered to be the major threats to coral reefs. Today, reefs face additional pressure from thermal stress and emergent diseases that are closely linked to global warming [1–8]. In the most damaging case to date, 16% of the world’s reefs were impacted in 1997–1998 by a regional-scale bleaching event that affected the Great Barrier Reef, vast tracts of the western Pacific, the Indo-Australian Archipelago, and the Indian Ocean [1, 10–11]. Climate-change projections indicate that similar events will reoccur with increased frequency in the coming decades [2, 12], highlighting the urgency of developing improved tools for managing reefs in the face of escalating threats [4–5, 13–15].

Here, we experimentally examined the resilience of coral-dominated assemblages on the Great Barrier Reef and the processes underlying a phase shift to macroalgal dominance (Figure 1A). We define resilience as the ability of reefs to absorb recurrent disturbances (e.g., from cyclones, outbreaks of predators, or coral bleaching events) and rebuild coral-dominated systems. Loss of resilience can lead to a phase or regime shift to an alternate assemblage that is typically characterized by hyperabundances of fleshy seaweeds or other opportunistic species. The experiment was designed to simulate the depletion of large predatory and herbivorous fishes caused by chronic overfishing [16–21] and to investigate their role in the regeneration of reefs after recent mass bleaching and the mortality of corals (see Experimental Procedures). The scale and timing of the experiment allowed us to measure the postbleaching dynamics of a rich coral assemblage (77 species represented by 4569 colonies were recorded by the end of the experiment), and its location provided us with a baseline comparison of an unusually intact fish fauna on heavily grazed reef crests within an established no-take area of the Great Barrier Reef Marine Park. This is the first replicated herbivore-exclusion experiment that explicitly examines herbivore-algae-coral interactions in the context of climate change. We demonstrate that exclusion of larger fishes profoundly erodes the resilience of coral reefs and their ability to regenerate after bleaching, with

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major implications for reef ecology, conservation, and management.

**Experimentally Induced Phase Shift**

Our experimental exclusion of fishes replicated the paucity of medium and large fishes that is characteristic of chronically overfished reefs in S.E. Asia, the Caribbean, and elsewhere [16–19]. The biomass of herbivorous fishes inside cages (Figure 1A) was reduced to levels seven to ten times lower than in adjacent partial cages and open plots (0.45 ± 0.08 [S.E.], 4.29 ± 2.81, and 3.12 ± 1.24 kg/m² per hr of video observation, respectively, F = 7.79, p < 0.001; Figure S1 in the Supplemental Data available with this article online). In response to the experimental exclusion of larger herbivorous fishes, benthic assemblages in the cages followed a fundamentally different trajectory over time, with upright fleshy macroalgae rather than corals and algal turfs becoming predominant, mimicking similar responses on many overfished and polluted reefs worldwide [4–8, 20–21].

In the aftermath of massive loss of corals on Orpheus Island in 1998 [10], roving herbivorous fishes continued to suppress the biomass of macroalgae and thus facilitated the recruitment of corals (Movie S1). In the partial cages and open plots where fish grazing was uninhibited, the cover of macroalgae (primarily the calcified red alga, *Galaxaura subfruticulosa*) averaged only 4.1% and 1.7% during the experimental period (n = 16 censuses), ranging up to a maximum of 10% and 7%, respectively (Figure 2A). In contrast, algal cover in the cages far exceeded the two control treatments throughout the experiment, reaching up to 91%, and averaging 56% ± 21% (S.E.) after 30 months (repeated-measures ANOVA, F = 3.82, p < 0.05; Figure 2). By the end of the experiment, algal biomass in the cages was 9 to 20 times higher than in partial cages and open plots (1363 ± 234, 146 ± 49, and 68 ± 28 g wet weight per m², respectively; ANOVA, F = 20.8, p < 0.001). Over time, the species composition of macroalgae in the cages diverged dramatically from the other two treatments (Figure S2). Dense thickets of *Sargassum*, previously absent on the reef crest, grew to 3 m in height inside the cages, with maximum densities of greater than 1000 plants (holdfasts) per 25 m² and a biomass of up to 8.55 kg wet weight per m² (Figure 1B and Movie S2). Cover and species composition of crustose coralline algae also diverged in the three experimental treatments (Figure 1C and Figure S3).

**Herbivory Boosts the Resilience of Coral Assemblages to Global Warming**

In tandem with the changes in macroalgae and corals, the trajectory of coral reassembly after the 1998 bleaching event diverged markedly in the fish-exclusion cages compared to the partial cages and open plots (Figure 2B). Initially, the most prevalent taxa (accounting for >80% of coral cover) were branching *Porites*
cylindrica, massive Porites spp. (especially P. lobata and P. rus), and massive faviids (principally heads of Goniastrea, Favia, and Montastrea spp.) that had survived the bleaching event 2 years prior to the initiation of the experiment. Alcyonacean soft corals and branching hard corals, particularly a diverse suite of Acropora species, were virtually eliminated from shallow sites by bleaching [10], and only a few small recruits were present (<0.1% cover) when the experiment began in 2000.

In the fish-exclusion cages, total coral cover grew from 6.0% ± 0.8% (S.E.) to 7.7% ± 1.0% after 30 months. Coral cover increased much more quickly inside the partial cages and open plots, reaching 19.2% ± 2.3% and 20.2% ± 2.2% in the three treatments (see text for analysis). Census dates were the same for all treatments and are slightly staggered in the plots for clarity. Error bars are SE.

The divergence in coral cover among treatments was attributable to both lower recruitment and higher mortality of established corals after the experimental reductions of fish biomass (Figures 3A and 3B). A total of 1062 new recruits from 26 coral genera were recorded in the three treatments at the end of the experiment (Figure 1D). Overall, coral recruitment in cages was approximately two-thirds lower (39 ± 11 recruits per 25 m², compared to 108 ± 26 for partial cages and 118 ± 21 in the open plots; ANOVA, F = 150.9, p < 0.001; Figure 3A). Acropora, which was virtually eliminated in 1998 from the reef crest at Orpheus Island by bleaching [10], accounted for 246 of the recruits, representing 23% of the total. The dominant adult genus, Porites, had only two recruits in the cages, compared to 19 in partial cages, 26 in open plots; F = 12.49, p = 0.003). Similarly, Acropora recruits were three times more abundant in partial cages and open plots (F = 7.7, p = 0.011). In contrast, Fungia and Euphyllia were more abundant inside cages, where together they comprised 18% of the recruits compared to only 3% in each of the two other treatments. A principal component analysis summarizes the striking divergence in the composition of coral recruits in cages compared to partial cages or open plots (Figure 4). Recruit assemblages in the partial cages and open plots were indistinguishable.

The suppression of coral recruitment inside cages is unlikely to have been an experimental artifact for two reasons. First, the considerable size of the cages and
the absence of a roof minimized caging effects (e.g., because of reduced water flow or shading from the cage structure). Light levels in the cages supported luxuriant algal growth, and macroalgae and juvenile fishes recruited in great numbers into them. Second, the partial-cage treatment did not show an intermediate reduction in numbers of newly recruited corals (Figure 3B). Juvenile *Fungia* and *Euphyllia* (and the coralline alga, *Mesophyllum purpureascens*) are normally found in deeper water and on shaded vertical surfaces and are rare on shallow reef crests. Consequently, the divergent response by juvenile corals among the experimental treatments (Figure 4) is more likely to reflect a range of tolerances to shading by the dense stands of *Sargassum* than differences among experimental treatments in the rate of delivery of larvae by currents.

Mortality rates of older coral colonies, which had survived bleaching and were already established when the experiment began, were more than double in the cages (24.2% after 30 months compared to 9.8% for partial cages and 11.3% for open plots (Figure 3B; RM-ANOVA, \( F = 4.29, p < 0.05 \)). Recruitment was insufficient to counter these losses in the cages, where the total number of coral colonies decreased by an average of 72 ± 32 per 25 m\(^2\) (a 26% decline). In contrast, counts of corals increased by 43 ± 21 (16%) and 39 ± 24 (14%) per 25 m\(^2\) in partial cages and open plots, respectively. In addition to changes in mortality of corals, we also recorded significant differences in sublethal indices of coral condition attributable to indirect impacts of herbivorous fishes (see Supplemental Data).

**Conclusions**

**Implications for Coral-Reef Management**

The spatial and temporal scales of our experiment (300 m\(^2\), 30 months) was sufficiently large that we successfully generated a phase shift to macroalgal dominance. The increased numbers of small fishes inside the cages may be due partially to reduced rates of predation or to the enhanced settlement and migration of juveniles into the dense algal canopies that formed after the exclusion of large roving herbivores. Ironically, the small herbivores and detritivores that dominated the cages may have promoted blooms of fleshy seaweeds by removing filamentous epiphytes and sediment from the surfaces of macroalgae that were too large or well-defended for them to consume. These findings provide robust experimental evidence for trophic cascades or top-down control—changes in the structure of foodwebs and species composition (e.g., enhanced recruitment of fishes and increased algal biomass) due to reduction in the abundance of medium and large fishes [18, 20, 22]. After 30 months, we removed the mesh from cages to allow entry once more to roving herbivores and predators. Cover of macroalgae in the newly accessible cages declined rapidly because of intense grazing, from 53% to 13% after 12 days and to approximately 0 after 30 days [23]. Juvenile fishes in the former cages declined much faster than the algae, by 96% after only 3 days, presumably because of predation. In the Caribbean, Mumby et al. [24] tested the potential importance of marine no-take areas for safeguarding parrotfish and their ability to control blooms of turf and fleshy seaweeds. They found a greater biomass of parrotfishes and less macroalgae inside a no-take reserve, consistent with the experimental results presented here (although the abundance of adult and juvenile corals was not reported). Our large-scale experiment provides direct evidence that overfishing of herbivores affects more than just the targeted stocks and can also influence the resilience of coral reefs to climate change.

Process-oriented research, exemplified by the experimental manipulations presented here, provides a more rigorous basis for coral-reef management than conventional approaches. In particular, the current focus on descriptive mapping and monitoring of reefs needs to be substantially broadened for better understanding of critical processes that underlie resilience. Our results demonstrate that loss of coral-reef resilience can be readily quantified with several metrics (e.g., depletion of key functional groups of fishes, reduced rates of coral recruitment and population regeneration, sublethal impacts, etc.). Furthermore, our findings show that local management efforts in support of resilience can afford significant protection against threats that are much larger in scale. Preventing coral bleaching is not a tractable management goal at meaningful spatial or temporal scales, and a long-term solution will require global reductions of greenhouse gases over decadal timescales. On the other hand, supporting resilience in anticipation of bleaching and other recurrent disturbances can be achieved locally by changing destructive human activities (e.g., overfishing and pollution) and thereby reducing the likelihood of undesirable phase shifts. Achieving this outcome will require the linking of ecological resilience to social and governance structures and involve scientists, other stakeholders, environmental managers, and policy makers [25–26]. A resilience-based approach represents a fundamental change of focus, from reactive to proactive management, aimed at sustaining the socioeconomic and ecological value of coral reefs in an increasingly uncertain world.
Experimental Site and Experimental Treatments

The fish-exclusion experiment was undertaken on the inner Great Barrier Reef, in Pioneer Bay on the leeward coast of Orpheus Island (18°36′S, 146°29′E), a high-island approximately 10 km offshore from the Australian mainland. Like many continental reefs in Australia, the reef fauna is highly diverse, with a benthos dominated by massive and branching scleractinians and alcyonacean soft corals. The water is turbid (typical horizontal visibility is 5–8 m), and the typical tidal range is 3–3.5 m. The sheltered reef fringing the lee of the island seldom experiences breaking waves except during rare storms and cyclones. Fishing has been banned in Pioneer Bay since 1987.

The three experimental treatments were (1) four 5 × 5 m fully-meshed roofless cages for excluding all large and medium fishes (Figure 1C), (2) four partially meshed cage controls that afforded access across 50% of each perimeter to control for any effects of the caging structure, and (3) four open plots. Each of the 12 replicates was 25 m² in area. The cage and partial cage framework consisted of eight 4-m-tall vertical lengths of 50-mm-diameter tubular steel (at each corner and midway along each side), three horizontal lengths along each side at the bottom, middle, and top, and an internal cross of tubing that connected horizontally between the four middle vertical uprights. We anchored the vertical tubes by sliding them over a 2 m steel bar that was hammered halfway into the substrate and cemented in place. Eight stays were also attached to each cage to prevent them from lifting. A door to each cage (2 × 0.8 m) provided access at all tide levels. The 4 m height of the cages and partial cages obviated the need for a roof because they extended a few decimeters above water at high tide, and the base always remained submerged. The plastic mesh on cages and partial cages (1 cm² for the bottom 2 m, and 2 cm² for the top 3 m) was scrubbed every 7–10 days to prevent fouling. A weighted net sealed the bottom. After the 30 months, we removed the mesh screens and partial cages and closely followed the immediate response of fishes and macroalgae. Diadema sea urchins are rare at this location. Three were removed from the cages (100 m³) at the start of the experiment.

Numbers and Sizes of Herbivorous Fishes

The abundance of herbivorous fishes in each treatment was measured after 28 months with 90 hr of high-resolution remote video. In each of the 12 replicates, partial cages, and open plots, five randomly placed 1 m² quadrats were censused for 90 min with remote video cameras (so that diver effects could be eliminated). Recording was undertaken within 90 min of high tide between 1000 and 1600, with randomly allocated times among treatments. Fish were identified to species, and their body lengths were recorded and converted to biomass with standard length-weight regressions.

Response of Macroalgae and Coralline Algae

Fleshy macroalgae and noncoralline crusts were identified in situ to genus, and their abundance in each of the 12 plots was estimated on a six-point categorical scale (0 = “absent,” 1 = “rare,” 2 = “uncommon,” 3 = “common,” 4 = “abundant,” and 5 = “dominant”). A total of thirteen censuses were made, and two were made after the removal of the mesh. In addition, the percentage of macroalgae cover was measured from 16 photographic censuses (0.25 m² resolution) of 2 × 2 m quadrats located centrally within each cage, partial cage, and open plot. Abundances of crustose coralline algae were measured initially and after 26 months from photographs of 33 permanently marked 10 × 10 cm quadrats (two to four quadrats distributed among each of the 12 replicate plots). At the final census, macroalgae were first removed from the quadrats, by brushing to expose overgrown corallines, and then the quadrats were rephotographed. Samples of live and dead corallines were collected for taxonomic identification.

Responses of Corals

Coral cover, survivorship of colonies, and cover of macroalgae was estimated from digital photographs (0.25 m² resolution, 16 censuses) of 2 × 2 m areas positioned centrally within each of the 12 experimental areas. In addition, all corals greater than 1 cm in the experiment were identified (to species, where possible) and mapped initially in September 2000 and again in April 2003, with a grid of 100 × 0.25 m² quadrats covering each of the 12 experimental plots. A comparison of the two censuses yielded data on recruitment (arrival of new colonies) and coral composition.

Coral tissue thickness, an index of biomass and physiological condition, was measured with calipers after 2 years in 64 colonies of Porites cylindrica from within two cages and outside. Those colonies from within cages were (1) positioned at least 10 cm away from the nearest clump of macroalgae, (2) shaded or (3) partially overgrown by macroalgae. Reproductive output of corals was measured in 90 experimental fragments of Montipora digitata that were placed 17 weeks before spawning outside and within two cages, the latter either positioned in the open or beneath clumps of macroalgae (principally Padina). After 14 weeks, fragments were collected and decalcified for an estimation of egg size, number of eggs per polyp, and number of reproductive polyps.

Supplemental Data

Supplemental Data include additional Experimental Procedures, three figures and two movies and are available with this article online at http://www.current-biology.com/cgi/content/full/17/4/360/DC1/.

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Implications of climate and environmental change for nature-based tourism in the Canadian Rocky Mountains: A case study of Waterton Lakes National Park

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Abstract

In western North America, Rocky Mountain national parks represent a major resource for nature-based tourism. This paper examines how climate change may influence park tourism in the Rocky Mountain region by focusing on both the direct and indirect impacts of climate change for visitation to Waterton Lakes National Park (WLNP) (Alberta, Canada). A statistical model of monthly visitation and climate was developed to examine the direct impact of climate change on visitation. The model projected that annual visitation would increase between 6% and 10% in the 2020s and between 10% and 36% in the 2050s. To explore how climate-induced environmental change could also indirectly affect visitation, a visitor survey was used (N = 425). The environmental change scenarios for the 2020s and 2050s were found to have minimal influence on visitation, however the environmental change scenario for the 2080s (under the warmest climate change conditions) was found to have a negative effect on visitation, as 19% of respondents indicated they would not visit the park and 37% stated they would visit the park less often. The contrasting result of the two analyses for the longer-term impact of climate change was a key finding. The management implications of these findings and methodological challenges associate with climate change impact assessment for tourism are also discussed.

Keywords: Climate change; Environmental change; National parks; Tourism; Canada

1. Introduction

Nature-based tourism is an important element of the tourism industry in North America. National parks in Canada and the United States are central components of this tourism market (Jones & Scott, 2006). Eagles, McLean, and Stabler (2000) estimated that there were over 2.6 billion visitor days in parks and protected areas in Canada and the United States in 1996, 300 million of which occurred in national parks.

A sizable share of park tourism in North America is concentrated in national parks located in the mountainous regions of western Canada and the United States. In Canada, approximately 65% (or ~10 million visits) of all national park visits in 2003 occurred in the six national parks located in the Rocky Mountains (Parks Canada, 2004); 10 million people visited the four US-based Rocky Mountain national parks during the same year, representing 17% of all national park visits in the United States in 2003 (National Park Service, 2005). The economic impact of tourism in the Rocky Mountain region is equally significant. Tourism-related expenditures by visitors to three mountain national parks in the Province of Alberta (Banff, Jasper and Waterton Lakes) were estimated to exceed US$765 million (Alberta Economic Development, 2000). In the United States, Yellowstone National Park generates an estimated US$2 billion in economic benefits for the states of Montana, Wyoming and Idaho (Gourley, 1997).

Climate directly affects nature-based tourism by limiting when specific recreation and tourism activities can occur...
(e.g. season length with snow cover or open water), recreation/tourism demand (e.g. proportion of people willing to swim or camp under certain conditions), and the quality of a recreation/tourism experience (utility) (e.g. hiking in warm, sunny conditions versus a cold rain or extreme heat).

In the Rocky Mountain region, this climatic influence manifests itself through a marked seasonality in park visitation; nearly two-thirds (64%) of annual person visits in Canada’s six mountain parks occur during the traditional warm-weather months of May–September (Parks Canada, 2004). Scott and Suffling (2000) and Scott (2003) argue that any direct changes in the length and quality of warm-weather tourism seasons induced by global climate change could present opportunities to increase visitation in national parks in this region. Visitor increases precipitated by a warmer climate would have benefits for park revenues and the economies of gateway communities near each park, but could also exacerbate visitor-related environmental pressures in some high-visitation mountain national parks in Canada and the United States.

Climate indirectly affects nature-based tourism by impacting the physical resources that define the nature and quality of natural environments on which mountain tourism depends (i.e. climate-induced biophysical change). Any changes in the natural characteristics of mountain environments could negatively influence tourism by reducing the perceived attractiveness of the region’s mountain parks (Elsasser & Bürgi, 2002; Scott, 2003; Wall, 1992). For example, drought conditions during the summer of 1988 contributed to widespread forest fires in Yellowstone National Park, which resulted in evacuations of campgrounds and seasonal visitor accommodations being closed 4 weeks earlier than normal (Franke, 2000). Total annual visits to Yellowstone in 1988 were reduced 15% (compared to 1987) and park officials estimated that the forest fires resulted in a loss of tourism-related economic benefits of US$60 million (Franke, 2000).

Progress has been made in documenting climate-induced biophysical changes in the mountain region of western North America and a number of studies have examined the potential biophysical impacts of climate change to the end of the 21st century. Analysis of biome-scale vegetation modeling suggests that under climate change mountain parks in this region would experience both latitudinal and elevational environmental changes with the potential for species reorganization and loss of biodiversity (Scott, Malcolm, & Lemieux, 2002). In an analysis of Glacier National Park (Montana), Hall and Farge (2003) projected that forests would advance upslope approximately 20 m per decade through 2050. While similar advancements in the tree line are projected for Yellowstone National Park, the results of vegetation modeling further suggested that the range of high-elevation species would decrease, some tree species would be regionally extirpated and new vegetation communities not currently found in the park would emerge (Bartlein, Whitlock, & Shafer, 1997).

Glaciers in western North America are important tourist attractions for mountain parks, but they have been retreating over the past century and are projected to continue to do so under climate change. Glacier National Park has lost 115 of its 150 glaciers over the past century and scientists estimate that the remaining 35 glaciers will disappear over the next 30 years (Hall & Farge, 2003). Similar projections have been made for glaciers in Canada’s Rocky Mountain parks with glaciers less than 100 m thick projected to disappear over the next 30–40 years (Brugman, Raistrick, & Pietroniro, 1997). If such glacier retreat is realized in the Rocky Mountains, Glacier National Park would lose its namesake and the very resource that defines it. Scott (2005) also argued that the projected glacial retreat in Canada could severely hinder the snocoach tours (specially designed buses take visitors onto the Athabasca glacier) that attract 600,000 visitors annually to the Columbia Icefields between Banff and Jasper national parks.

Mountain ecosystems depend on fire for regeneration, but forest fires pose a threat for park tourism. Under climate change, the frequency and severity of forest fires in the mountainous region of western Canada is projected to increase. Vegetation and fire behavior modeling by Li, Flannigan, and Corns (2000) suggested that west-central Alberta would experience a one-point shift in the fire fuel moisture code under a mean temperature increase of 4°C (+7.2 F), which would contribute to an increase in the frequency of fires that burn more than 1000 ha. Stocks et al. (1998) projected that the geographic area in western Canada currently designated as having an ‘extreme’ fire danger would expand in the 2050s. Similar regional projections were made by Flannigan et al. (2001) and Weber and Flannigan (1997). If the fire season becomes more severe under climate change, it is possible that visitors to mountain parks may experience more restrictions on their activities (e.g. campfire bans; trail and park closures).

As lakes and streams warm, temperature-induced habitat loss and range shifts are projected to occur, contributing to losses in recreationally valued fish populations. Research on the thermal habitat for salmonid species in the Rocky Mountain region of the United States found that a projected 4°C (+7.2 F) summer warming in the region would reduce habitat area by 62% (Keleher & Rahel, 1996). Simulation studies of cold-water fish habitats revealed that the southern boundaries of some cold-water fish in the United States could move 500 km northward under climate change (Magnuson, 1998). Increases in lake and river temperatures could place pressure on cold-water fish species in the Rocky Mountain region, thus providing opportunities for the geographic expansion of cool- and warm-water species that have higher temperature tolerances.

There remains a great deal of uncertainty as to how potential climate change impacts on seasonality and mountain landscapes would impact park visitation around the world and in western North America. In the only
empirical study to examine the potential impact of climate change on mountain park tourism, Richardson and Loomis (2004) assessed the direct and indirect impacts of climate change on visitation to Rocky Mountain National Park (RMNP) (Colorado, USA). Regression analysis of historical monthly visitation data (1987–1999) and four climate variables for the park’s peak and shoulder seasons was used to model the current influence of climate on park visitation and the projected changes under climate change for the 2020s. Richardson and Loomis (2004) found that visitation to RMNP would increase 7–12% in the 2020s as the warm-weather tourism season was extended. Visitors to the park were also surveyed to determine how their visitation patterns (number of visits and duration of stay) might change under a range of early environmental change scenarios. Although hypothetical, the environmental change scenarios were partially developed on the basis of climate change studies of the potential environmental impacts in the park. Environmental changes in the 2020s were found to have minimal effect on visitor behavior, as visitation was projected to increase between 10% and 14% under the two environmental scenarios used in the visitor survey.

With the results of their regression analysis of visitation data and tourist survey projecting similar increases in park visitation, Richardson and Loomis (2004) concluded that climate change through the 2020s would have a positive effect on park visitation in the Rocky Mountains, and suggested that the results for RMNP would be representative for a number of mountain parks in the United States (Glacier, Grand Teton and Yellowstone) and Canada (Banff, Jasper and Waterton Lakes).

The Richardson and Loomis (2004) study only examined the potential impacts of early stages of climate change projected for the 21st century and thus the implications of much greater warming and environmental change projected for the latter half of the century (IPCC, 2001) remain an important knowledge gap. While climate change scenarios for the 2020s have the most relevance for contemporary tourism planning and there remains substantial uncertainty about the magnitude of long-term climate change projections (i.e. 2050s, 2080s) (IPCC, 2001), the potential implications of longer-term changes should be explored for strategic relevance to park managers, the tourism industry and broader climate change policy (i.e. the costs of impacts verses mitigation). It remains uncertain whether Richardson and Loomis’ (2004) findings would be representative of the potential influence of long-term climate change on mountain park visitation. Will climate change-induced seasonality and environmental changes continue to have a positive effect on visitation or will environmental changes projected for mountainous regions in western North America towards the end of the 21st century begin to have a negative impact on visitation?

This paper presents an empirical assessment of climate change and related environmental change. Using a similar methodological approach to Richardson and Loomis (2004), the specific objectives of the study were to: (1) develop a model of climate and park visitation in order to examine the implications of changed climatic conditions on future visitation levels and seasonal visitation patterns; (2) survey park visitors to determine how a range of potential climate-induced environmental changes may influence their intention to visit the park and visitation frequency; and, (3) compare the implications of direct climatic changes and indirect climate-induced environmental changes on park visitation at three time steps commonly used in climate change impact assessments (2020s, 2050s and 2080s). Conceptually, the analyses of the potential direct and indirect impacts of climate change are considered separate and therefore the respective methodologies and results are presented individually and then compared in the final discussion section.

2. Data and research methods

The focus of this study is Waterton Lakes National Park (WLNP), which is located along the foothills of the Canadian Rocky Mountains in southwestern Alberta adjacent to the Canada–US international border. WLNP is described by Parks Canada as a place ‘where windswept mountains rise abruptly out of gentle prairie grassland’ (Parks Canada, 2005). WLNP, the smallest of Canada’s six Rocky Mountain national parks (525 km; ~130,000 acres), receives nearly 400,000 visitors annually (Parks Canada, 2004); 84% of annual visitation occurs between May and September, clearly demonstrating the seasonal influence of climate. WLNP is also bordered on the south by Glacier National Park (GNP) in the state of Montana, and together the two parks make up the Waterton-Glacier International Peace Park (WGIPP). Established in 1932, WGIPP protects a diverse ecosystem comprised of grasslands, pine and aspen forests, alpine meadows and glacier-covered mountains.

2.1. Climate and park visitation

Monthly recorded visitation data (number of person visits) from WLNP for the 1996–2003 (January–December) tourism seasons were used in this study to assess the influence of climate on visitation. Analysis of the direct influence of climate on visitor levels was undertaken using data from the nearest Meteorological Service of Canada climate station that contained suitable monthly observations for 1996–2003 for use in modeling the relationship between current climate and visitation and a quality historical climate record (i.e. 1961–1990) to establish a climatic baseline for the climate change impact assessment.

Climate data met quality standards for inclusion in the Meteorological Service of Canada’s national archive and there were no prolonged periods of missing data.
Monthly level temperature and precipitation data were obtained for the airport station in the City of Lethbridge (Alberta), located approximately 125 km northeast (≈79 mile) of WLNP.

The climate change scenarios used in the analysis were developed from monthly global climate models (GCM) available from the Government of Canada’s Climate Impacts and Scenarios (CCIS) Project. The scenario data available from CCIS are constructed in accordance with the recommendations set out by the United Nations Intergovernmental Panel on Climate Change (IPCC) Task Group on Scenarios. Climate change projections for three future timeframes were examined, each of which were based on a 30-year period of climate data (i.e. the 2020s represent the period 2010–2039; the 2050s represent 2040–2069; and, the 2080s represent 2070–2099). All scenarios represent climate changes with respect to the 30-year baseline climate (1961–1990).

In accordance with IPCC guidelines for climate change impact assessments, more than one GCM and greenhouse gas (GHG) emission scenario were used in this study to represent uncertainty in future climatic conditions in the study area. The two climate change scenarios utilized in this study were the National Center for Atmospheric Research (NCAR) GCM with a B2 emission scenario (a low greenhouse gas emission future) and the Center for Climate System Research (CCSR) GCM with an A1 emission scenario (a high greenhouse gas emission future).

The two climate change scenarios used in this study (NCARPCM B21 and CCSRNIES A11) were selected from among 19 available scenarios; the NCARPCM B21 scenario generally projects the smallest increase in annual mean temperature in the region this century (+2°C; 3.6°F), while the CCSRNIES A11 scenario projects the largest increase (+7°C; 13°F).

Visitor projections for WLNP under a changed climate were undertaken using statistical analysis. First, multivariate regression analysis using three monthly level temperature variables (maximum, minimum and mean temperature) and one monthly level precipitation variable (total precipitation) was employed to establish the nature and strength of the empirical relationship between climate and monthly person visits during the 1996–2003 tourism seasons. The resultant regression model was then applied to monthly climate data from the Lethbridge climate station for the 1961–1990 baseline to establish visitation in a climatically ‘normal’ year, against which future climate change scenarios (also averages of 30-year model runs) would be compared. This step should not be interpreted as an attempt to model past visitation to WLNP between 1961 and 1990. Rather, the purpose of running the regression model with climate data from 1961 to 1990 is to establish visits in a ‘climatologically average’ year during the baseline period; 30 years is the standard used by climatologists to establish ‘current’ climatic averages. Under the assumption that current visitation patterns would remain unchanged in the future (i.e. the analysis does not account for other factors that influence visitation—population growth, transportation costs), the regression model was then run with both climate change scenarios (NCARPCM B21 and CCSRNIES A11) for the 2020s, 2050s and 2080s to assess the potential impact of climate change on the number and seasonal pattern of visitation in WLNP with respect to the 1961–1990 baseline.

Visitor data made available for this analysis from Parks Canada provided counts of total visits and did not distinguish the origin of visitors (i.e. local, regional or international) or the activities visitors participated in. Without specific information correlating activities (e.g. skiing, hiking) with visitors, the projections put forward in this study will emphasize the implications of climate change for seasonal visitation resulting mainly from a longer and improved season for warm-weather tourism activities. The winter tourism season is less important to WLNP (less than 10% of total annual visitation) than warm-weather tourism season, so although snow and ice-based recreation is anticipated to decrease under a warmer climate (Scott, 2003, 2005), losses are expected to be compensated for through larger gains in warm-weather recreation.

### 2.2. Environmental change and visitation

Any projected change in WLNP’s seasonal pattern of visitation resulting from a changed climate will not occur in isolation, as visitation will also be indirectly influenced by climate-induced changes in the natural environment that nature-based tourism depends on. Analysis of the indirect impact of climate change on park visitation was undertaken in this study through a visitor survey that explored how climate change-induced environmental change in WLNP might affect visitor behavior.

Three environmental change scenarios were developed for WLNP to reflect the types of environmental changes and the magnitude of change anticipated to occur in the Canadian Rocky Mountains over the next century. A range of environmental changes identified in Scott and Suffling’s (2000) climate change impact assessment of Canada’s national parks were considered in each scenario, including wildlife and vegetation compositions, forest fire occurrences, the number of glaciers lost, water temperatures and the probability of campfire bans. The scenarios were hypothetical, but were based on available scientific literature on documented environmental changes in the Rocky Mountains of western North America and projected biophysical changes from region-specific climate change impact assessments in the scientific literature (Brugman et al., 1997; Hall & Farge, 2003; Stocks et al., 1998), and other studies of environmental changes in the Rocky Mountains (Harding & McCullum, 1997; McCarty, 2001; McDonald & Brown, 1996; Rhemtulla, Hall, Higgs, & MacDonald, 2002).

Once created, each scenario provided a plausible story about the anticipated environmental changes in WLNP in the 2020s, 2050s or 2080s (under the warmest climate change scenarios) with respect to current conditions.
Unlike Richardson and Loomis (2004) who examined implications of potential environmental changes into the 2020s, this study continued to further examine how projected climate change into the 2050s and 2080s might affect tourist behavior. Survey participants were asked to reflect on each scenario as a holistic package of environmental changes and consider whether they would still visit WLNP if the identified changes occurred, and, if so, whether they would visit more or less frequently. Participants were also asked whether they would visit a mountain park other than WLNP if the types and magnitude of long-term environmental changes identified for WLNP were not occurring elsewhere (i.e. destination substitution). Participants could not respond differently to individual potential changes (i.e. warmer lake temperatures were desirable, but loss of glaciers was unacceptable). The scenarios provided in the survey instrument are presented in Fig. 1.

The presentation of the environmental change scenarios in the visitor survey was similar to Richardson and Loomis (2004) to provide consistency for comparison of results and because pre-tests suggested that graphics and numerical change estimates would be easier for respondents to interpret than a detailed text-based scenario. The participants in the WLNP survey were not informed of the time period that each environmental change scenario represented (i.e. changes under the warmest climate change scenario for the 2020s, 2050s or 2080s). This was done to avoid biasing the participant’s responses (e.g. ‘I will not be alive in 2080, so these impacts are less important or will not change my intention to visit’). Before the survey was
administered, it was pre-tested \((N = 30)\) and appropriate revisions were undertaken.

The visitor survey was administered in WLNP during the summer of 2004 (July 24–August 20) at a variety of locations throughout the park including campgrounds, scenic rest stops, public beaches, backcountry hiking areas and visitor parking lots. A range of survey locations was selected with the purpose of identifying visitors engaged in different recreation and tourism activities. At each location, visitors were approached randomly (i.e. every third person or group) and informed of the study’s purpose and asked if they were willing to complete the survey. If visitors were in a group, the person with the birthday closest to the survey date was asked if they would participate. The random sampling approach ensured that each visitor had an equal opportunity to participate. Willing participants took the survey with them and were asked to return it by mail in the pre-paid return envelope provided. Mail-return surveys were used in order to give respondents adequate time to consider the three environmental change scenarios and so as not to interfere with people’s activities. A total of 800 surveys were distributed in WLNP; 425 usable surveys were returned (53% response rate).

3. Results

3.1. Direct influence of climate and climate change on visitation

Similar to other national parks in the Rocky Mountains of western North America, there is marked seasonality to WLNP’s visitation. Fig. 2 illustrates monthly visits to WLNP for the 2000–2003 tourism seasons. Person visits were found to be highest during the summer months of July and August (≈110,000 per month) when most Canadians have school or work-related vacations (i.e. institutional seasonality). The winter period between November and March traditionally experienced the lowest levels of visitation (≈6000 visits per month).

Comparison of WLNP’s tourism seasons revealed some notable inter-annual variability in visitation. Annual person visits declined 8% in 2003 over 2002 with the most significant monthly reductions occurring in July (−7%), August (−17%) and September (−15%). Officials with Parks Canada have suggested that the reductions were in response to forest fires in a number of mountain parks during the hot and dry summer of 2003 in western North America. Although WLNP did not experience fires, Parks Canada acknowledged that fire-related park closures (e.g. trails, access roads) and wide-spread media coverage of the fires in nearby Canadian (e.g. Kootenay, Jasper) (Parks Canada, 2003; Winks, 2003) and US (e.g. Glacier National Park) (Mann, 2003; Newhouse, 2003) mountain parks deterred visitors from WLNP.

Although institutional seasonality (i.e. summer school holidays) plays an important role in seasonal visitation to WLNP, Fig. 2 demonstrates that climate (i.e. natural seasonality) is also important factor. A primary objective of this study was to estimate the potential direct impact of climate change on annual person visits to the park. In order to assess the potential impact of climate change on visitation, a multivariate linear regression analysis involving four monthly climate variables (maximum, minimum and mean temperature and total precipitation) was undertaken. The regression analysis resulted in a one-variable model \((r^2 = 0.67)\) with minimum temperature being identified as the strongest predictor of monthly visits \(t\)-statistic = 13.83; \(p < 0.005\). Fig. 3 (Graph A) demonstrates the nature and strength of the relationship between total monthly visits and minimum temperature in WLNP.

Closer examination of the linear regression model in Fig. 3 (Graph A) revealed two important limitations. First, the regression model continued to project an increase in visits as minimum temperature increased. Conceptually, at some critical temperature conditions would likely become too uncomfortable for most people (i.e. heat stress), and rather than increasing, visitation would begin to stabilize and then decline. Similarly, at some minimum temperature, visitation would decline to zero. Second, the relationship between temperature and visitation to WLNP is clearly not linear and distinct climate–visitor relationships are evident at different times of the year. July and August are characterized by visitation levels in excess of 80,000 and little variation with temperature, while visitation in all other months was less than 60,000 but varied substantially with temperature. Due to the combined effect of natural and institutional seasonality, a second regression analysis was undertaken in which visitation in WLNP’s peak season (defined as July and August; visits >80,000) and shoulder (defined as September–June; visits <80,000) tourism seasons was modeled separately.

Fig. 3 (Graphs B and C) illustrates the nature and strength of the regression models for WLNP’s peak and shoulder seasons. Minimum temperature was found to be the strongest predictor of visits in each season, with a strong relationship in the shoulder season \((r^2 = 0.94)\), but a weak relationship during the peak season \((r^2 = 0.01)\). Since the \(r^2\) value in the peak summer season was low (0.01), future changes in minimum temperature are projected to have minimal impact on visitation to WLNP during the peak
season. The regression expressions used in this study were:

Shoulder season (September–June) = $3.95x^3 + 194.34x^2 + 2903.20x + 19,536$,

Peak season (July and August) = $-230.59x + 102,253$.

When the regression models were run with the two climate change scenarios, the resulting projections suggested that WLNP would expect to experience an increase in visitation under a warmer climate relative to baseline conditions. In the 2020s, total annual visits were projected to increase 6% (NCARPCM B21) to 10% (CCSRNIES A11) over the modeled 1961–1990 baseline average (418,358 person visits annually). These results were consistent with Richardson and Loomis’ (2004) regression analysis of visitation (+7% to 12%) in RMNP under their 2020s climate change scenarios. In the 2050s, increases were projected to range between 10% (NCARPCM B21) and 36% (CCSRNIES A11), which translates into an additional 42,000–152,000 person visits to WLNP annually. The strong growth in visitation in the shoulder season resulting from climate conditions becoming more suitable for warm-season tourism during the spring (April–June) and fall (September–November) could lead to an extended peak tourism season in WLNP (Fig. 4). In the 2080s, the number of people visiting WLNP was projected to increase 11% over current baseline conditions under the least-change scenario (NCARPCM B21) and increase 60% under the warmest scenario (CCSRNIES A11).

If these findings are suggestive of the long-term effects of a more suitable climate for tourism in WLNP, to say nothing of future increases from population growth in Canada and the United States (which were not included in this analysis), the implications for visitation and park management are substantive, but can be interpreted either positively or negatively. As for the benefits, elevated visitor levels would result in higher revenues for Parks Canada, primarily from the collection of additional entrance and recreation service fees in WLNP. The Town of Waterton (population of ~150), located inside WLNP, and communities around the park would also benefit from higher visitor levels as long as growth could be achieved in a sustainable manner. Higher visitation and a longer tourism season would also contribute to higher operating costs and enhance existing visitor-related environmental pressures. Increased need for services (e.g. campgrounds) and visitor management could put stress on existing staff resources in WLNP. The additional stress placed on existing park infrastructure such as roads, trails, water systems and waste management could also lead to increased maintenance costs, as it is anticipated that infrastructure will need more frequent upgrades and/or repair with higher use. Implications of higher visitation for the park’s ecological integrity mandate remain uncertain.

3.2. Influence of climate change-induced environmental change on visitation

The results of the above analysis of the potential direct impact of a changed climate suggested that WLNP could
experience substantial increases in visitation as the climate in the Canadian Rocky Mountains becomes more favorable for warm-weather tourism and recreation. The regression model only considered the implications of a changed climate for visitation to WLNP, yet the park is also anticipated to undergo concurrent biophysical changes as the climate warms. To explore how park visitation may be affected by climate change-induced environmental change a survey was administered in WLNP that asked visitors to consider the frequency of future visits under three hypothetical scenarios of environmental change in the park.

More than 75% of survey respondents indicated that viewing mountain landscapes and viewing wildlife were either ‘important’ or ‘extremely’ important to their decision to visit WLNP. By contrast, less than 15% of respondents indicated that recreational activities including golf, fishing and boating were important for motivating them to come to WLNP. These results suggest that WLNP’s mountain landscape is a critical factor in attracting visitors, and any environmental changes that diminish that landscape could have a negative effect on park tourism.

Fig. 5 summarizes the projected impact of climate change-induced environmental change in WLNP on park visitation. After considering the environmental changes outlined in scenario 1 (~2020s), the majority of respondents (99%) indicated that they would still visit WLNP and 10% indicated that they would visit more often. These results were consistent with Richardson and Loomis’ (2004) analysis of visitation in RMNP under their 2020s scenarios. In WLNP, a majority of respondents (97%) again indicated that they would visit the park if the environmental changes in scenario 2 (~2050s) were realized, however 14% of those who said they would still visit, would visit less often.

For many respondents, the environmental changes described in scenario 3 (~2080s) represented a critical threshold of acceptability. Of the 425 respondents, 19% indicated that they would no longer visit WLNP if the environmental changes in scenario 3 were realized. An additional 37% of respondents indicated they would visit less often. With most respondents indicating that they would not visit or would visit the park less often, it is possible that the considerable environmental changes projected to occur later this century may contribute to reduced annual visitation at WLNP. This finding represents a notable contrast to the large increase in visitation projected by the previous analysis that only considered the impact of a direct change in climate later in the century (i.e. 14–60% increase in the 2080s). The results of the survey suggest that long-term environmental changes may diminish the attractiveness of WLNP’s landscape to some visitors and offset some of the potential gains in visitation made possible by an extended and climatically improved warm-weather tourism season.

The projected environmental changes in WLNP later this century could negatively impact visitation by reducing the attractiveness of the park landscape and thereby providing a comparative advantage to other mountain parks where the impacts of climate change may be less pronounced. When respondents were asked if they would visit another mountain park in the region not experiencing the changes in scenario 3 (~2080s), 34% of respondents indicated they would go to the alternative destination.

4. Discussion and concluding comments

This case study examined the potential impact of climate change on nature-based tourism in WLNP, one of Canada’s Rocky Mountain national parks. The study used two separate methodological approaches to examine the potential direct and indirect impacts of climate change on park visitation. A multi-year data set of monthly observed visitation were used to develop regression-based climate–visitation models in order to explore how a changed climate could directly impact the timing and number of annual visitors to WLNP. A visitor survey was then used to explore how climate change-induced changes to WLNP’s natural landscape might indirectly influence future visitation.

The climate-visitation model projected that annual visitation to WLNP would increase under all of the climate change scenarios examined, but particularly under the warmer scenario (CCSRNIES A11). The direct affect of a changed climate was projected to increase visitation to WLNP by 6–10% in the 2020s. The findings for the 2020s are consistent with Richardson and Loomis (2004) and together are likely representative of other Rocky Mountain national parks in Canada (e.g. Banff, Jasper and Waterton Lakes) and the United States (e.g. Glacier, Grand Teton and Yellowstone). If climate change scenarios for the 2050s were realized, visitation to the park was projected to increase 10–36%. For the same time periods (2020s and 2050s), the visitor survey revealed that climate change-induced environmental changes would likely have minimal impact on visitation, as most respondents (> 90%) indicated that they would not change their intentions to visit WLNP or the frequency of their visits. As such, the direct effect of climate change in lengthening and improving the warm-weather tourism season would appear to be the dominant impact on visitation in the early to mid-decades of the 21st century.
A key finding was the contrast between the climate-visitaton model and the visitor survey with regard to the impact of climate change late in the 21st century. The climate-visitaton model projected the direct impact of a changed climate would increase visitation to the park (+11% to 60%—2080s), but the survey found that the indirect impact of climate-induced environmental change in the park might reduce visitation, with 56% of respondents indicating that they would no longer come to the park or would visit less often if the environmental changes in scenario 3 (~2080s warmest scenario) were realized.

Although climate-induced environmental change was found to have a potentially important negative impact on visitation under scenarios for the latter part of the 21st century, caution needs to be taken when interpreting these survey results. There is much greater uncertainty in longer-term scenarios because of greater uncertainties in climate change projections (IPCC, 2001) and how society and tourist preferences may evolve over such long timeframes. As such, while the environmental changes posed in scenario 3 may result if the warmest (high emission) climate change scenarios for the 2080s were realized, if a low-emission future were realized, environmental change closer to that outlined in scenario 2 may occur. Notably, scenario 2 has virtually no impact on visitors' intentions to visit the park.

The long-time frames involved also present critical methodological challenges. Although respondents were not given the time frames of the scenarios in the survey, the large magnitude of environment change portrayed in scenario 3 would take several decades to manifest (~2080s or later). The majority of people visiting the park in the 2080s would not be born until the 2040s. By this time, some of the environmental changes projected (e.g. disappearance of the glaciers) may have already occurred and consequently the sense of loss felt by a respondent in 2005 may not be shared by a visitor born in the 2040s. It currently remains uncertain whether these 'future visitors' will be deterred from visiting mountain parks in western North America if they have never experienced the landscape attributes that current visitors use to define and measure the quality of mountain experiences. The lived experience of visitors in the 2080s will be very different (perhaps unimaginably so) than those in 2005, and therefore it remains uncertain whether the negative impact of environmental change on visitation later in this century would occur to the extent the survey results suggest.

Understanding the behavior of 'future tourists' is an important conceptual barrier for climate change impact and adaptation studies in the tourism sector (and other economic sectors—e.g. farmers, planners) to overcome. Regardless of whether respondents in 2005 can accurately represent the behavioral intentions of visitors in the 2050s or 2080s, the salient findings of the survey component of this study stand—the magnitude of environmental change required to become meaningful for altering people's intentions to visit Rocky Mountain national parks is very substantial, and based on current understanding, is several decades away even under the warmest climate change scenarios. That is not to suggest climate change and climate-induced environmental change should not be a concern to park managers, but rather the near-term focus of climate change adaptation in mountain parks should be on managing the impacts of climate change for conservation mandates (Hannah et al., 2005; Scott & Lemieux, 2005) and increased visitation over the next 20–30 years, resulting from an extended and climatically improved warm-weather tourism season.

Mountain tourism is clearly influenced by the climate (Scott, 2005), and this study has provided important insight into the potential direct and indirect impacts of climate change on visitation in one Rocky Mountain national park in western North America. Given the economic importance of national parks to nature-based tourism in North America, it is hoped that this study will encourage further research into the impact of climate change on park tourism in other regions of Canada, the United States and world-wide.

References


