Review:

No 'silver bullet': multiple factors control population dynamics of European purple sea urchins in Lough Hyne Marine Reserve, Ireland

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ABSTRACT

Two-decade-long monitoring studies at Europe's first statutory marine reserve—Lough Hyne in SW Ireland—indicate that benthic communities are rapidly changing. Populations of the ecologically important purple urchin (*Paracentrotus lividus*) have fluctuated widely, most recently with a population boom in the late 1990s, followed by a mass mortality that persists to the present day. Eight general hypotheses have been proposed to account for the urchin decline including cold temperature limiting reproduction, ephemeral algal exudates disrupting urchin fertilization, low larval availability (due to over-harvesting and/or episodic recruitment), high mortality of settlers and juveniles due to hypoxia, hyperoxia or predation (a trophic cascade hypothesis), and increased mortality due to pathogens (stress hypothesis). The cold-temperature and the trophic cascade hypotheses appear unlikely. The remaining hypotheses, however, all seem to play a role, to some degree, in driving the urchin decline. Ulvoid exudates, for example, significantly reduced urchin fertilization and few larvae were found in plankton tows (2012–2015), indicating low larval availability in summer. Whilst settling urchins regularly recruited under shallow-subtidal rocks until 2011, no settlers were found in these habitats from 2011 to 2014 or in field experiments (2012–2018) using various settlement substrata. Seawater quality was poor in shallow areas of the lough with extreme oxygen fluctuations (diel-cycling hypoxia), and 1-day experimental exposures to DO values <1 mg L^{-1} were lethal to most juvenile urchins. Multiple increases of the predatory spiny starfish (*Marthasterias glacialis*) population in recent decades may also have contributed to the demise of the coexisting juvenile urchins. Finally, urchins of all sizes were seen suffering from dropped spines, tissue necrosis, or white-coloured infection, suggestive of stress-related pathogen mortality. There was a paucity of broken tests, indicating limited predation by large crustaceans; the large number of adult urchins 'missing' and few *P. lividus* tests on the north shore points to possible urchin removal by poachers and/or starfish predation. While these ecological, environmental, and anthropogenic processes occur on many open coast rocky shores, many are exacerbated by the semi-enclosed nature of this fully marine sea lough due to its limited flushing. Multiple factors, including low larval availability and rapidly expanding starfish populations, coupled with degraded habitat quality (ephemeral algal mats and extreme oxygen fluctuations), indicate that the purple urchin populations will not recover without an improvement in the water quality of Lough Hyne Marine Reserve, the restocking of urchins and protection from poaching.

Keywords: Paracentrotus lividus, sea urchins, mass mortality, marine reserve, *Marthasterias glacialis*, hypoxia

1. Introduction

Many echinoderms exhibit 'boom-and-bust' population dynamics (reviewed by Uthicke et al., 2009), exemplified by the European purple urchin (*Paracentrotus lividus*) which has shown rapid to catastrophic decreases in density followed by little recovery (Barnes *et al.*, 2001, 2002; Trowbridge *et al.*, 2011). This species has also exhibited intense proliferations, resulting in barren grounds and regime shifts (e.g., in the Mediterranean Sea: Sala et al., 1998a; Bonaviri et al., 2009; Agnetta et al., 2013, 2015). Mass mortalities of urchins and other marine taxa are becoming better documented and/or more frequent (Feehan and Scheibling, 2014a,b; Fey et al., 2015). For example, the green urchin (*Strongylocentrotus droebachiensis*) in maritime Canada, the long-spined urchin (*Diadema antillarium*) on Caribbean reefs, its congener in the Pacific, *D. africanum* in the subtropical E. Atlantic, the purple urchin (*S. purpuratus*) in the NE Pacific have all exhibited mass mortalities in recent decades (Pearce and Hines, 1979; Miller and Colodey, 1983; Lessios, 1988, 1995; Karlson and Levitan, 1990, Benítez-Villalobos, 2009; Girard et al., 2012; Hendler, 2013; Clemente et al., 2014; Feehan and Scheibling, 2014a,b). Populations of *P. lividus* have crashed within weeks to months on Mediterranean shores and in the Canary Islands and more slowly, over years in Ireland (Boudouresque et al., 1980; Barnes et al., 2002; Boudouresque and Verlaque, 2007; Trowbridge et al., 2011; Girard et al., 2012; Yeruham et al., 2015). Furthermore, Jurgens et al. (2015) reported mass mortalities of echinoderms (and chitons) across 100 km of NE Pacific shore. The drivers of such mass mortality events are understudied although several have been proposed. Outbreaks of pathogens or disease, increased seawater temperature, environmental degradation, or a complex interaction between multiple stressors have been implicated in the crash of urchin populations (Foster and Schiel, 1988; Steneck et al,. 2002; Knowlton, 2004). Given the many factors affecting urchin population dynamics (and their additive or multiplicative effects), the timings of mass mortality events are largely unpredictable.

Some studies of the consequent changes that occur in rocky subtidal communities have been based on comparisons between pairwise surveys (historical vs. contemporary) made many years apart. For example, O'Sullivan and Emmerson (2011) took this approach to suggest marine reserve designation of Lough Hyne led to establishment of stronger trophic cascades and altered community structure and dynamics. However, as pointed out by Dayton et al. (1998) after a 25-year study of kelp beds, oscillations and changes in subtidal communities can exhibit extremely long-term regime shifts. The drivers of present-day distributions may lie decades in the past. Without surveys at an appropriate time scale (at least annually), it is thus hard to investigate causes and mechanisms of change. Fortunately, there have been some long-term subtidal annual surveys, which have noted changes in echinoderm populations. Hereu et al. (2012), for example, surveyed populations of *P. lividus* in the northwest Mediterranean, over a period of 20 years, demonstrating changes in relation to habitat and the drastic effect of a violent storm which reduced population densities to the lowest levels observed during the study. Filbee-Dexter and Scheibling (2014) reviewed long-term studies that monitored changes in the alternation between urchin barrens and kelp forests. Their models demonstrated the importance of feedback loops that stabilize each state. In some areas, transitions between these states have different thresholds when moving from kelp forest to urchin barrens or barrens to kelp forest. In other areas, transitions may be triggered by large-scale oceanographic changes.

In the present study, we investigated the causes of changes in the abundance of the urchin *P. lividus* in Lough Hyne, Ireland. Thanks to the work of J.A. Kitching and his collaborators, this lough has been one of the sites where experimental studies of marine ecology evolved (over the last 70 years, see, e.g. Ebling et al., 1948; Kitching et al., 1952; Hawkins et al., 2016), and where many field techniques were pioneered (Paine, 1994; Kearney, 2011). Many of the early measurements of change in the urchin populations in the lough were made by Kitching and co-workers (Ebling et al., 1966; Kitching and Thain, 1983), when 'drastic falls' in numbers were observed between years. As well as documenting changes in the *P. lividus* population, we have measured major changes in the abundance of the spiny starfish

Marthasterias glacialis, as both have shown extreme fluctuations on similar scales to those discussed by Uthicke et al. (2009). In parallel to our studies of the intertidal zone (Little et al., 2017a, 2018), we also quantified the abundance of major species of macroalgae and macro-invertebrates in the shallow subtidal region over the period 1994-2014, with supplemental species data from 2015 to 2017.

The loss of ecologically significant species, such as urchins, can have important consequences to communities (Personnic et al., 2014; Thibaut et al., 2017), particularly where they are keystone, bolt, or rivet species (*sensu* Power and Mills, 1995; Schiel, 2006). Past research at Lough Hyne indicates that the urchin, *P. lividus,* was ecologically important (Kitching and Ebling, 1961, 1967; Kitching and Thain, 1983). Furthermore, this species has been described as a keystone species in the Mediterranean region (Prado et al., 2009, 2012). Recent research at Lough Hyne on the trophic consequences of losing such a major herbivore dismissed the urchin's importance (O'Gorman and Emmerson, 2009; O'Sullivan and Emmerson, 2011); but these researchers investigated an already declining and unhealthy population of urchins with insufficient consideration of the spatio-temporal variation in the decline and alternative explanations (Trowbridge et al., 2011; *this study*). While it is unequivocal that the purple urchin population in Lough Hyne has declined catastrophically in the last two decades (Barnes et al., 1999, 2001, 2002; Verling et al., 2002; Trowbridge et al., 2011; *this study*), the timing and proposed drivers remain matters of debate and, in several cases, based on circumstantial evidence. There are at least eight published hypotheses that may account for the urchin decline in Lough Hyne and on other Irish shores; these are discussed below. This variety of theories suggest that there is no simple, 'silver bullet' explanation, as sought by previous colleagues (e.g. Barnes et al., 2001, 2002; O'Sullivan and Emmerson, 2011; Boudouresque and Verlaque, 2013), and the cause of the decline is undoubtedly multi-causal.

2. Hypotheses and alternatives

2.1. Low temperature limiting reproduction and, hence, larval production

The purple urchin occurs on NE Atlantic shores from Scotland and Northern Ireland to southern Morocco and the Canary Islands as well as throughout the Mediterranean Sea (Boudouresque and Verlaque, 2013). However, within Ireland, *P. lividus* lives at the eastern edge of its range (see Hiscock et al., 2004 for range map redrawn from Forbes). The urchins have been reported from Whitehall in County Cork to Malin Head (Southward and Crisp, 1956; references therein) with a single verbal record of the species outside of Lough Hyne at nearby Baltimore (pers. comm. from Renouf to Southward and Crisp).

The urchins live in water temperatures that vary from 10° to 15°C in winter and 18° to 25°C in summer, although many of the Atlantic locations are cooler. The lethal upper and lower limits for English Channel urchins are 29°C and 4°C, respectively (Boudouresque and Verlaque, 2013). The reported seawater temperature range in Ireland and, thus, within Lough Hyne fits well into the species' habitable temperature range. Sea urchin fecundity is known to be temperature-dependent; summer seawater temperatures <13°C inhibit urchin spawning (González-Irusta et al., 2010) although the extent to which this varies with acclimatization to local conditions has not been explored. Studies of Irish populations of *P. lividus* have shown that spawning occurred in January – March and August – September in Bantry Bay, May – July in Ballynahown, and June – July in Glinsk (Crapp and Willis, 1975; Byrne, 1990) (see Fig. 1A for localities).

Kitching and Thain (1983) suggested that the warm summers of 1975 and 1976 may have led to the high urchin recruitment and peak numbers in 1979. Furthermore, Barnes et al. (2001, 2002) suggested that the *P. lividus* population declined in Lough Hyne in response to cooler seawater during years that the Atlantic summer temperatures were suppressed by the global effects of a Pacific ENSO event which constrained urchin reproduction. However, those latter authors measured seawater temperature at 1-m depth at an open-water buoy in the lough, not at the water depth or shore location where urchins were actually found. To counter these data, we hypothesized that shallow-water temperatures on the shore would be warmer in summer than open-water temperatures, and that temperature thresholds for urchin reproduction were met during most Irish summers.

2.2. Extreme weather causing significant mortalities

Extreme weather phenomena have caused major reductions in *P. lividus* populations in different parts of the species' range, including: record heat or increasing temperatures, unusually cold temperatures, exceptional rainfall, and intense storm winds and waves (Bouxin, 1964; Turon et. al., 1995; Fernandez et al., 2003, 2006; Garrabou et al., 2009; Girard et al., 2012; Hereu et al., 2012; Boudouresque and Verlaque, 2013; Fey et al., 2015; Yeruham et al., 2015). We, therefore, predicted that harsh winters and/or exceptional rainfall would be the most probable mechanism to cause urchin decline at Lough Hyne. If extreme weather events were observed in the Met Éireann records for the meteorological station at Sherkin Island (Fig. 1A) near the lough, and did cause significant mortalities, we would generally expect to see an abundance of intact urchin tests on the seabed (although if high winds were the causal mechanism, we would expect a high density of broken tests). Given that urchins have low tolerance of reduced salinities, extreme rainfall effects would be localized to the upper edge of the urchin's tidal range and the northern-most area on the western shore where streams and/or seeps flow into the lough. Furthermore, such events would cause an acute impact on urchin populations, not a chronic one.

2.3. Reduced urchin fertilization due to ulvoid exudates

Ephemeral green and brown algae are proliferating on shores worldwide, including Irish shores (review by Lyons et al., 2014) and those of Lough Hyne (Trowbridge et al., 2011; Little et al., 2018).

Ulvoid algae (e.g. *Ulva intestinalis*) are opportunistic species that tend to bloom in masses (forming 'green tides'), sometimes covering entire shores in many places around the world. Ulvoids contain chemicals that can be exuded when the algae encounter stressful conditions during aerial desiccation (e.g. Van Alstyne et al., 2011). These exudates—such as dimethylsulfoniopropionate (DMSP), dopamine, reactive oxygen species (ROS), and their breakdown products—could have negative effects (e.g. reduced fertilization, larval growth and metamorphosis or increased mortality) on the coexisting adult and larval stages of marine invertebrates and some macroalgae (Nelson et al., 2003; Van Alstyne et al., 2014, 2015; Peckol and Putnam, 2017; Vázquez et al., 2017). The gametes (sperm and eggs) of the Pacific sand dollar (*Dendraster excentricus*) were relatively insensitive to exudates of a related ulvoid (Vázquez et al., 2017) but fertilization success and larval development were significantly altered. If reduced fertilization success were occurring, we would expect to see a paucity of juvenile benthic urchins in recent years with the increase in ephemeral algae.

2.4. Low larval availability

Paracentrotus lividus gonads are a commercially prized human food through much of the urchin's geographic range, including Ireland (reviewed by Boudouresque and Verlaque, 2013). Moylan et al. (1998) reported the over-exploitation of urchins in western Ireland in the 1970s and early 1980s. Declan O'Donnell (previous warden of Lough Hyne Marine Reserve; *pers. comm.*) suggested that the known decline in wild urchins may have caused low larval production and supply in SW Ireland, including Lough Hyne. Furthermore, residents of southwest Cork have illegally harvested urchins from within the lough (*confidential pers. comm.*), presumably contributing to low local larval levels.

Low larval availability could also occur if the urchin species experienced recruitment failure within the lough for several years and/or episodic recruitment from outside the lough. Many marine invertebrates as well as macrophytes exhibit periods of low recruitment followed by episodic pulses of high recruitment (e.g., Ebert, 1982; Pearse and Hines, 1987; Menge, 1991; Yoshioka, 1996; Sam and Keough, 2012). Many species of sea urchins exhibit highly variable recruitment dynamics (e.g., Ebert, 1982; Pearse and Hines, 1987; Turon et al., 1995). For example, Ebert (1982) reported one strong recruitment class in *Strongylocentrotus purpuratus* in Sunset Bay, Oregon during a 20-year study period. Pearse and Hines (1987) reported a single strong recruitment pulse of *S. purpuratus* during a decade-long study in California. In neither case was the pulse correlated with water temperatures or upwelling indices (Ebert, 11982; Pearse and Hines, 1987). Episodic recruitment, whether as a result of oceanographic events influencing larval supply or biotic interactions, contributes to high variation in adult abundance.

Given the longevity of the urchin's benthic stages ranges from about 6 to 9 years in Ireland (Crapp and Willis, 1975) and up to 15 years depending on locality (Boudouresque and Verlaque, 2013), a bottleneck at the larval stage, and thus poor recruitment, would cause a rapid population decline as the oldest age-classes senesced. If this process were occurring, we would expect to see a paucity of juvenile benthic stages of urchins in recent years, and an imbalance in the urchin size-frequency distribution.

2.5. Increased predation intensity and/or changed predator guilds

Changes in predator regimes may significantly affect urchin populations through trophic cascades (O'Sullivan and Emerson, 2011; Galasso et al., 2015). Many predators reputedly consume *P. lividus* in different parts of its range, including starfish, crabs, hermit crabs, trigger fish, sparids, Ballan wrasse and other labrids (Muntz et al., 1965; Ebling et al., 1966; Kitching and Ebling, 1967; Kitching and Thain, 1983; Bernárdez et al., 2000; Sala and Zabala, 1996; Sala et al., 1998a,b; Guidetti 2004, 2006; Hereu et al., 2005; Figueriedo et al., 2005; Guidetti and Dulčić, 2007; Bonaviri et al., 2009, 2012; Gianguzza et al., 2009, 2016; Galasso et al., 2015; Boudouresque and Verlaque, 2013; McAllen, *pers. comm.*). As well reviewed by Galasso et al. (2015: 1), however, trophic cascades 'are no means certain to occur in all locations.'

By comparing pairwise surveys in 1962/3 and 2010, O'Sullivan and Emmerson (2011) concluded that the 1981 marine reserve designation caused an increase in predatory crabs and starfish that in turn led to a decline in *P. lividus*. However, they provided no direct evidence for 1981 (or shortly thereafter) being the date for change in ecological regime (e.g., actual change in fishing pressure and/or predation intensity), and ignored numerous other alternative drivers (see Trowbridge et al., 2011; references therein). In our study, we documented long-term temporal changes in the shallow-water abundances of purple urchins as well as the generalist predator, the spiny starfish *Marthasterias glacialis.* Savy (1987) found that *M. glacialis* in Mediterranean France consumed purple urchins (which constituted approximately half the diet); Bonaviri et al. (2009), Galasso et al. (2015), and other researchers have documented this for Italian shores. Furthermore, Verling et al. (2003) reported these shallow-water juvenile starfish have an opportunist diet and do consume purple urchins in Lough Hyne.

Based on this predation hypothesis, we would expect to see a decline of large adult urchins and/or an increase of smashed or cracked/broken tests (crustacean predators) or intact tests (starfish or stress) on the seabed of the lough (see Boudouresque and Verlaque, 2013). Thus, the expected pattern would be similar to that produced by severe wind events.

2.6. High mortality of early post-settlement stages

The high mortality of purple urchin settlers has been well studied in the Mediterranean (López et al., 1998; Tomas et al., 2004; Prado et al., 2009, 2012; Bonaviri et al., 2012). In addition to the attrition of larvae and settlers due to predation, juvenile urchin stages are vulnerable to declining physical conditions which may be exacerbated in the semi-enclosed (though fully marine) Lough Hyne. The development of extreme low oxygen conditions in the lough (Trowbridge et al., 2017a; Little et al., 2018), for example, may initiate mortality of early urchin life stages; dissolved oxygen (DO) levels <1.5 mg L^{-1} are lethal to larval purple urchins (Saco-Alvarez et al., 2010). Furthermore, low DO values prevent green urchins from becoming reproductively mature (Siikavuopio et al., 2007). If this process were occurring, we would expect to see a paucity of juvenile stages in recent years (post-2010) at Lough Hyne. The resulting pattern of urchin size-frequency distribution would be similar to that expected for the low larval availability hypothesis.

2.7. Increased mortality due to pathogens or parasites

Mass mortality of urchins around the world has occurred due to virus and/or bacteria outbreaks with physiological stress (e.g., increased seawater temperatures) being a contributory trigger (e.g. Boudouresque et al., 1980; Gilles and Pearce, 1986; Lessios, 1988, 1995; Scheibling et al., 2010; Girard et al., 2012; Boudouresque and Verlaque, 2013; Wang et al., 2013; Clemente et al., 2014; Feehan and Scheibling, 2014a,b). Semi-enclosed bodies of seawater with low flushing rates (such as Lough Hyne: Johnson et al., 1995; Jessopp and McAllen, 2007) would be particularly vulnerable to such pathogen outbreaks. Although purple urchins have exhibited population crashes due to bald-urchin disease (or something similar) in Mediterranean locations (see Zizzo et al., 2004; Boudouresque et al., 1980; Boudouresque and Verlaque, 2013) and the Canary Islands (Girard et al., 2012), the existence of the disease has not yet been confirmed for Ireland (but see Trowbridge et al., 2011 for discussion of its probable occurrence in Lough Hyne). If pathogens were the cause of mortality in the lough, we would expect to see either a variety of sizes of ailing urchins and/or intact tests on the seabed of the lough, or a narrow range of sizes if stress were size dependent (as indicated by Girard et al., 2012).

Parasitic infection is another possibility, although insufficiently studied. In Norway, extensive population declines of the green urchin (*Strongylocentrotus droebachiensis*) were caused by parasitic nematodes. In fact, Hagen (1992: 207) suggested the locally distributed nematode ‘could terminate population outbreaks of the urchin’ though Skadsheim et al. (1995) questioned the parasite’s importance.

2.8. Mortality due to toxic microalgal blooms

Dinoflagellate blooms have been well studied around Ireland and their toxic effects have been reported for invertebrates (e.g. Cross and Southgate, 1980; Leahy, 1980; Silke et al., 2005). In particular, the dinoflagellate *Karenia mikimotoi* (formerly called *Gymnodinium aureolum*) has been implicated in repeated shellfish and fish mortalities in Europe (Tangen 1977; Ottway et al., 1979; Cross and Southgate, 1980; Silke et al., 2005; Davidson et al., 2009) and worldwide (O’Boyle and Silke, 2010; O’Boyle et al., 2016). Numerous blooms of this dinoflagellate were recorded in 1978 and 1979 in SW Ireland (O'Boyle and Silke, 2010) and around Sherkin Island (Fig. 1A) in Roaringwater Bay in 1985, 1993, 2001, 2004, and 2010 (Dale and Murphy, 2014). Leahy (1980) reported that 14% of the *Paracentrotus* surveyed in a belt transect at Dunmanus Bay during a dinoflagellate bloom (*K. mikimotoi*) were dead; 50% of the urchins encountered during the general shore survey were also dead. There was also an exceptional bloom of the dinoflagellate in western Ireland in 2005 (Silke et al., 2005; O'Boyle et al., 2016). O'Boyle et al. (2016) emphasized how seasonally stratified marine areas are particularly vulnerable to such dinoflagellate blooms. Thus, Lough Hyne with its well-established seasonal stratification, particularly in the Western Trough (Kitching et al., 1976; McAllen et al., 2009) may be affected by harmful algal blooms more than neighbouring coastal areas outside the lough.

In the Mediterranean Sea, there have been numerous recent reports of blooms of the benthic dinoflagellate *Ostreopsis ovata*. In laboratory experiments, Privitera et al. (2012) demonstrated that this species caused significant mortality of *Paracentrotus* juveniles. This dinoflagellate or its congeners have been reported also from Atlantic Portugal and Spain so its spread to SW Ireland is possible. Mass mortalities of urchins have occurred in New Zealand and Brazil from *Ostreopsis* (Shears and Ross, 2009). It was beyond the scope of this study to test the 'toxic bloom' hypothesis in Lough Hyne.

These hypotheses are not necessarily mutually exclusive, nor exhaustive. In this review, we document the quantitative decline of the purple urchins in Lough Hyne, and then evaluate each of these hypotheses as potential causal agents in the context of our long-term, community-level investigation.

3. Description of the urchin populations

3.1. Site description

Lough Hyne is a semi-enclosed sea-lough in southwest Ireland (Fig. 1A) which is connected to the sea by narrow 'Rapids' (Bassindale et al., 1948). It was designated as Europe's first statutory Marine Reserve in 1981. In area it measures ~1 km^2, and consequent upon the small fetch, all shores are relatively sheltered. Most of the lough is less than 20 to 30 m in depth and, until recently, the benthic habitat was oxic most of the year. With the exception of three sets of subtidal rocky cliffs, the substrata below 10 m is primarily mud. The Western Trough is 40 to 50 m deep and becomes anoxic in summer and early autumn (reviewed by McAllen et al., 2009). No macrofauna dwells within the anoxic habitat until storm events disrupt the thermocline seasonally.

Because of the restricted inflow at the Rapids, the tidal cycle is asymmetrical, and the tidal rise and fall is restricted to about 1 m, so the intertidal zones are compressed (Rees, 1931, 1935; Bassindale et al., 1948; Little, 1991). Much of the intertidal is either bedrock or shingle, and varies from nearly vertical to shallow slopes (Ebling et al., 1960; Williams et al., 1999; Trowbridge et al., 2017b). There are several areas where small freshwater flows or seeps enter the lough and locally dilute the surface water (Rees, 1935). However, there is almost no dilution of the main body of the lough below a salinity of ~34 (Kitching, 1987). At times of exceptionally high rainfall, a localised, thin freshwater lens may form at the surface (Little, *pers. obs.*).

3.2. Study sites

Ebling et al. (1960) defined 20 monitoring sites around the lough above the Rapids (Fig. 1B) as part of their comprehensive description of the fauna and flora of the lough. Little et al. (1992) resurveyed the 20 sites in 1990 and 1991. Then 10 of the 20 original sites were selected (Fig. 1B) for annual monitoring. Each 'annual' site consisted of a 10-m length of rocky shore marked at each end with a stainless steel plate to enable exact recognition at future sampling dates. The other 10 sites ('historical' sites) were surveyed in 2014 as part of a related study (Trowbridge et al., 2017b).

3.3. Methods of monitoring juvenile and adult urchin populations

Purple urchins are only in a narrow depth range around the lough (low shore to about 5 m). In much of the lough, the urchin's lower depth range is constrained by (1) limited availability of rocky to boulder habitat and (2) steep substratum (subtidal cliffs). The centre of the lough does not function as a possible reservoir of urchins for two reasons: (1) it is almost exclusively muddy to gravelly substrata and (2) becomes seasonally anoxic (Kitching et al., 1970; McAllen et al., 2009). The remaining purple urchins in Lough Hyne occur within the interstices of boulders typically dominated by the green alga *Codium vermilara*, brown alga *Cystoseira foeniculacea*, and ephemeral algae. This 'cryptic' behavior such as hiding in crevices was noted by other colleagues at Lough Hyne (e.g., Verling et al., 2003) as well as on Italian shores (e.g., Sala and Zabala, 1996; Agnetta et al., 2013).

To monitor purple urchins in Lough Hyne, three different approaches were taken: (1) rock-turning in shallow subtidal habitats at 'annual' sites, (2) counting urchins along the entire north shore of the lough and (3) whole-lough snorkel surveys. The snorkel surveys provide a better estimate of living urchins, and estimates can be greater by an order of magnitude, when compared to those from shore-based observations (Trowbridge et al., 2011) or from boat-based estimates that have been made periodically for decades (e.g., Muntz et al. 1965; Kitching and Thain 1983; Kitching 1987; Barnes et al. 2002). Lough Hyne urchins have been shown to be most active during daytime (Ebling et al., 1966; Crook et al. 2000), making our urchin counts reliable, whereas the species is nocturnally active in the Mediterranean and migrates between habitats (Dance, 1987; Fernandez et al., 2001; Hereu et al., 2005).

For over two decades, shallow subtidal rocks were turned over annually to document the juvenile urchins that move down through the loosely assembled boulders and rock slabs (Ebling et al., 1966; Crook et al., 2000); all rock slabs were put back in their original positions within a few minutes which did not appear to significantly affect the benthic macrofauna (see Trowbridge et al., 2017b). This process was done in 1990/1991 (Little et al., 1992) and from 1994 to 2014 (*this study*) at 10 'annual' sites (Fig. 1B) each August to September. In addition, rocks were also turned in 2014 at 10 'historical' sites (Fig. 1B) that were previously surveyed only in 1955 and 1990/91 (see Trowbridge et al., 2017a). The test diameters of all urchins found were measured with calipers (± 0.1 mm). These latter 'historical' sites could potentially have higher urchin densities than at annual sites as the rock slabs had not been moved for two decades (i.e., lower disturbance). High densities of juvenile urchins would serve to reject the low-recruitment hypothesis and would support post-settlement mortality hypotheses.

Urchins were counted along the entire north shore of the lough from 1998 to 2014, during late August/ early September. Counts were made from the wall that forms the boundary of the lough, using binoculars when necessary, during low tide and light winds, and supplemented by counts taken from the water's edge. The entire north shore was typically surveyed on three separate days, though this was not always possible because of unfavourable visibility. The highest count was selected as being the best estimate of population size.

During annual snorkel surveys (2006–2017), most of the shoreline of the lough north and west of the Rapids was assessed in a non-destructive manner. The sector location and condition (the presence/absence of spines and/or lesions) of urchins was noted in the marked 108 sectors (Renouf, 1931; Fig. 1B). For dead urchins, the cause of mortality (Boudouresque and Verlaque, 2013) was evaluated based on whether the test had peristomial membranes and Aristotle's lantern present (assumed freshly dead, categorized as 'entire'); test 'intact' but spines, membranes, and jaws missing (potentially caused by starfish predation or lethal stress); or test broken or crushed (potentially by fish and/or crustaceans).

3.4. Changes in juvenile and adult urchin populations

The total number of purple urchins recorded at the monitoring sites increased from 1990 to 1995, stayed high (maximum total 145) through 1999, then began to decrease until there were only 7 recorded in 2014 (end of two-decade survey) (Fig. 2A). During supplementary sampling in 2015, 5 urchins were recorded at the 6 annual sites surveyed and 2 additional specimens at the historical sites surveyed. In 2016, we recorded 3 specimens: 1 at North Labhra, 1 at South Labhra, and 1 at Graveyard. The boom-and-bust pattern on the north shore was comparable to the monitoring-site pattern although the timing differed: *Paracentrotus* counts peaked at 2000 (a year later than at the monitoring sites) with 2,110 visible individuals, and declined to 0 in 2014 (Fig. 2D). Thus, since marine reserve designation (in 1981), Lough

Hyne purple urchins exhibited a *population boom* before the mass mortality; this boom was not reported by colleagues working on the same lough population (Barnes et al., 2002: fig. 1; O'Sullivan and Emmerson, 2011). When urchins were relatively common, they were observed on the top of rocks, and caused extensive 'graze patches' where ephemeral filamentous seaweeds were absent or rare. However, when the population declined, urchins were usually seen only underneath rocks, and visible graze patches were absent.

To evaluate the published assertion that the south basin urchins were 'locally extinct' (*sensu* Barnes et al. 2002), we divided our counts between north and south basin sites (Fig. 2B). Based on our under-rock surveys of shallow subtidal urchins in August/September, there were clearly many urchins present in the south basin in the early 2000s, and there was no significant difference in overall counts between the north and south basin sites (Student's t-test, t=0.431, df=38, P=0.669). Thus, our results reject the suggestion of local extinction of urchins in either basin in the past 25 years.

There was immense variation in number of purple urchins among monitoring sites and years (Fig. 3), indicating that the population decline was not caused by spatially or temporally discrete events. Based on urchin sizes and counts, the individual specimens recorded during one year were not generally the ones recorded the subsequent year. Maximum urchin numbers were seen at Westwood North, and minimum at North Island (Fig. 3A), but at most sites numbers were very low at the beginning and end of the survey period, with highest numbers in the late 1990s and early 2000s.

Population structure showed high variation in levels of recruitment from year to year (Fig. 2C, 3, 4). Maximum overall numbers of recruits (urchins with a test diameter <10 mm) occurred in 1996, but as a percentage of the population, maximum recruitment occurred in 2000, when ~30% of the population were this size. The lowest percentage (6%) occurred in 2010 and from 2011 to 2014 when there was no observed recruitment (Fig. 2C, 3–4). A few urchin recruits were seen in 2015, 2016, and 2017 but urchin densities were not increasing. Recruitment appeared spatially variable (Fig. 3B) with only 4 of the 10 sites having 5 or more recruits recorded per year. Codium Bay, a site directly north and west of the Rapids, had the highest recruitment (40 young-of-the-year urchins from 1996 to 2014). Westwood North, SE Labhra, and North Labhra also had similar recruitment (30-32 urchins) during the long-term study.

Based on two decades of monitoring surveys and a decade of snorkel surveys, we observed that the majority of dead urchin tests of *P. lividus* and the larger common urchin *Echinus esculentus* (Fig. 5) were intact. Most of the mortalities recorded were in the past decade, with a notable onset in 2009 at the monitoring sites (Fig. 5A). There was a paucity of urchin tests relative to the number of purple urchins disappearing each year on the extremely wave-sheltered shores of Lough Hyne. This absence was particularly noteworthy on the north shore where only a single urchin test was noted in a decade of snorkelling despite 2,110 living urchins being recorded there in 2000 (Fig. 2D). The majority of *P. lividus* tests recorded in late summer were on the west shore (Fig. 5B, 5E), where most of the remaining urchins live. Partial spine loss was frequently seen during snorkelling in living *E. esculentus* but not *P. lividus*; in contrast, 6 dead *P. lividus* were recorded under rocks in this condition (Fig. 5C, 5F). Two subtidal specimens were recorded with necrotic patches (Fig. 5F) and four low-shore individuals had white spots at the base of their spines (Fig. 5C). Finally, there were no observed cases of *P. lividus* or *E. esculentus* with broken or crushed tests (Fig. 5C, F) in the two decades of monitoring surveys or decade of snorkel surveys. However, the first author saw one case in September 2018 on the western shore close to a lobster den.

The north shore purple urchin population peaked in 2000 with over 1,000 urchins counted each year from 1998 to 2001 (Fig. 2D). However, by 2005 the population had declined 10-fold and by 2007, it had declined 100-fold. In 2009 and 2014, no purple urchins were seen on the north shore, even by snorkelling. It is therefore clear that a near-complete population disappearance had been recorded 10 to 15 years post-boom. We would not consider the decline to be a local 'extinction' *per se* because we did not turn the rocks under which most of the urchins dwell.

3.5. Short-term vs. long-term studies

Short-term 'snap-shot' evaluations of urchin dynamics in the lough (e.g. Barnes et al., 2002) may give an inaccurate perspective of the population. Barnes and colleagues suggested that the last population peak was in 1979 with no further recovery to 1999; they also suggested that after 2000, the population in the south basin was ecologically 'extinct' (no recorded urchins)—an extremely strong statement for a population that still occurred at most of our study sites. Our results (Fig. 2A) indicate a subsequent population peak in 1999 (monitoring sites) or 2000 (north shore). Furthermore, our results (Fig. 2B) show no significant difference in purple urchin counts between the north and south basins; thus, local extinction had clearly not occurred.

How do we resolve these dramatically different studies on the same urchin population? First, the two research groups surveyed at different times of year with the Barnes' surveys being conducted earlier in the summer than our late-summer surveys. If there were seasonal differences in urchin behaviour and/or environmental conditions in the benthos, significantly different patterns might be recorded. For example, if dissolved oxygen levels under rocks and in the interstices between rocks declined during the summer, the purple urchins would shift upward in the rock matrices or even move out of the cryptic habitats by late summer. Second, the differences may be due to the differing methodology of sampling. In order to make results compatible with historical data, Barnes et al. followed the methodology of Kitching (1987) which involved boat-based visual surveys. As pointed out by Kitching and Thain (1983), however, these surveys produced only 'an indirect indication of the number present. There were probably two to three times as many under rocks…'. In contrast, our studies involved a combination of snorkelling and turning rocks (Trowbridge et al., 2011, 2013, *this study*). Because of this difference, the earlier studies (Barnes et al., 2002) underestimated urchin numbers, although a population crash did occur years later.

4. Hypothesis testing

4.1. Cold-temperature hypothesis

4.1.1. Methods

Seawater temperatures were measured in the habitats and water depths where the urchins occurred. Temperature sensors were deployed at multiple locations along the western shore of the lough within the shallow (<1 m) subtidal habitats in which urchins occurred (Renouf sectors W9/10 to W22/23, Trowbridge et al., 2011). Sensors, attached to bricks with cable ties, recorded temperature every 1 to 2 hours (Onset Pendants) and every 15 minutes (Onset TidBits) from March 2014 to the present; data were downloaded twice a year. Although not every sensor was relocated each time, multiple replicate sensors were found and data downloaded each time. HOBO dissolved oxygen and temperature sensors (Onset U21-001) were deployed in various shallow locations around the lough (Codium Bay, East Goleen, North Labhra, etc.) and in Barloge Creek from September 2013 until the present. The data were downloaded, sensor caps replaced, and sensors recalibrated every 6 months.

In addition to these short-term, high resolution data, the surface water temperatures were measured manually (with a hand-held mercury thermometer) in the top 10 cm of the water column at the lough several times during every annual visit. Initially this was carried out from the Glannafeen Laboratory quay (S4/5); since 2000 to the present, temperatures were taken near the Gate Lodge on the north-east shore (N11).

4.1.2. Results

Since April 2014, seawater temperatures have varied annually by ~10–12°C in shallow subtidal areas on the western shore of the lough (Fig. 6) where the remaining urchins live. The mean minimum temperature in winter was ~7–8°C and the mean summer temperature was >15°C all three summers. In 2014 and 2015, the summer water was cooler than normal by about 2-3°C. However, in 2016, the seawater was ~15°C for much of the summer. Temperatures remained high until September/October with minimum temperatures in February and March. Although the mean values never fell below 5°C, individual sensors did record temperatures of 1-2°C. However, there is no strong evidence (since April 2014) that winter temperatures fell to the reported lethal level for purple urchins (4°C) or that summer temperatures rose to lethal limits (29°C) in habitats where urchins actually occurred.

How generalizable are these high-resolution values? Our long-term summer lough water temperature estimates on the south and north shore (Fig. 7) indicate that these values were typical for the last two decades with the exception of 1992 when the summer water temperature was anomalously low. Water temperatures were above the 13–15°C urchin spawning threshold for much of the summer and early autumn. In terms of the cold temperature in 2010 when the Goleen froze over, no observations were made of urchin mortality (larvae or adults) although one author (RM) noted extensive mortality of barnacles (no other authors were in Ireland during that time).

4.1.3. Conclusions

Oceanographic events that cause low seawater temperatures in Lough Hyne during the summer (e.g., 1992) did occur but the minimum temperature threshold for spawning was still attained in most years (Fig. 6-7). Furthermore, since ENSO, NAO or other oceanographic events are periodic and purple urchin longevity is ~8 years or longer, one cold winter or summer would not be sufficient to cause a population-level failure as opposed to a cohort or year-class failure. Thus, the cold-temperature hypothesis suggested by Barnes et al. (2001, 2002) would not be sufficient to explain the local situation on Irish shores.

4.2. Extreme-weather hypothesis

4.2.1. Methods

Meteorological data were obtained from Met Éireann for the weather station at Sherkin Island (Fig. 1A). The maximum air temperature, wind speed, gust speed, and rainfall for each month were calculated as well as the minimum air temperature. The wind values would be estimates only, due to the steep hills to the west of the lough that shelter the body of water from the south-westerly storm winds.

4.2.2. Results

There have been several periods in the past few decades with extreme weather. For example, there were several hot days in 1995, 1999, 2003 and 2006 (Fig. S1A) with 2003 being the most extreme year. During the extremely cold winters of 2010 and 2011 (Fig. S1B), air temperatures did drop well below the minimum threshold tolerances of purple urchins (4°C in the English Channel). Winter mortality of urchins may have occurred in 1996, 1997 and 1999 as well as 2010 and 2011 but examination of the urchin population (Fig. 3A) does not support a lough-wide mortality in any of the hot or cold years. Furthermore, the urchin population was extremely low before the 2010 and 2011 cold periods, indicating that the low temperature was not the primary causal driver of decline.

Daily rainfall was extremely variable (Supplemental Fig. 1A) with two days (in July 1997 and August 1998) with unusually high precipitation. However, urchin counts declined at only 4 of 10 sites in 1997 and 3 of 10 sites in 1998 (Fig. 3A). Thus, while rain may have contributed to urchin mortality due to low salinity, it may have been localized and acute, depending on the water depth of each sub-population of urchins.

In terms of severe wind, 1998 had the highest gust of wind (at the Sherkin meteorological station) and the maximum 10-min period of wind speed (Supplemental Fig. 1B). Hurricane Ophelia in September 2017 was clearly extreme. However, as noted above, the 1998 and 2017 events did not coincide with clear declines in purple urchin counts (Fig. 3A).

4.2.3. Conclusions

Extreme-weather phenomena have occurred during our long-term study. While such events may account for urchin disappearance at individual monitoring sites, they are insufficient to explain the overall population decline due to lack of spatial concordance (Fig. 3-4). The extremely cold winters of 2010/2011 may have killed many of the remaining urchins, but most of the decline occurred within the preceding decade. As most of the remaining urchins were on the partially shaded western shore, extreme hot weather effects were probably insufficient to account for the urchin demise; temperature sensors also refuted significant high temperatures as a primary causal factor. Extreme wind could cause waves to form in the lough and shift rocks under which urchins lived. However, most of the severe storms came from the south-west and the lough was partially protected by steep hills on the western side. Additionally, there were very few broken tests observed during subsequent sampling—which further indicates extreme wind events were unlikely to result in mass mortality events due to shifting substrata. A comparable conclusion was reached by Verling et al. (2005).

4.3. Algal-exudate hypothesis

4.3.1. Methods

Two species of green algae (Chlorophyta) proliferating in the lough were evaluated for potential effects on purple urchin reproduction. In September 2012, 9 sexually mature *Paracentrotus* were obtained from John Chamberlain’s Dunmanus Seafoods in Durrus, Co. Cork. The ephemeral alga *Ulva intestinalis* was collected from the east shore (Renouf sectors E11 and E19) and the perennial alga *Codium vermilara* was collected from the west shore, near the mouth of the Goleen (sector W24) on the day of the experiment or the afternoon before. Algal exudate acquisition was based on methods described by Van Alstyne et al. (2011). *Ulva intestinalis* and *C. vermilara* were blotted dry. Four pieces of 4.2 g (n=4 per algal species) were weighed and placed in small glass bowls. To simulate low tide conditions, bowls were placed outdoors in direct sunlight. After 2.5–3 h exposure, 300 mL of filtered seawater (FSW) were added to each bowl to simulate an incoming tide. Then, after 5 min, the macroalgae in all the bowls were removed. The water in all the bowls that had contained *U. intestinalis* was then mixed together into a single container labelled as '*Ulva* exudates' and the water in all the bowls that had contained *C. vermilara* was then mixed together into a single container labelled as '*Codium* exudates'. This methodology was comparable to that of other studies (e.g. Vázquez et al., 2017) where exudate concentrations used were determined to be within the natural range of exudation of the ulvoids (Van Alstyne et al., 2011, 2014).

The wet mass of purple urchins was determined and then individuals were shaken to stimulate natural spawning. For urchins that did not release gametes, we followed the standard procedure of inducing spawning (Gosselin et al., 2003) by injecting 20 µL of 0.5 M KCl per gram of wet weight through the perioral membrane of each urchins. Eggs were collected in beakers filled with cold FSW whereas sperm was collected 'dry' on Petri dishes; beakers and dishes were held in trays with ice to keep cold.

To determine the effects of *U. intestinalis* and *C. vermilara* exudates on fertilization of *P. lividus*, ~3 mL of eggs from 5 females were mixed in a beaker containing 300 mL of FSW. Then, ~3 mL of eggs from this stock were added to each of 20 plastic containers. Fifty mL of the *Ulva* exudate were then added to 5 containers (*Ulva* treatment); 50 mL of the *Codium* exudate were added to another 5 containers (*Codium* treatment); 10 containers were each filled with 50 mL of FWS (control treatment). The eggs were left to soak for 15 min. After the exposure, eggs in the *Ulva*-exudate and *Codium*-exudate treatments were filtered through a 41-µm mesh and then placed back in their containers with 50 mL of FSW. Sperm from two urchin males was mixed in a Petri dish and a drop of the mixture was diluted in 50 mL of FSW and well mixed. About 3 mL of the diluted sperm was then used to fertilize each container. After another 15 min, eggs in each container were filtered through a 41 µm mesh, placed back in the containers, and then preserved with 3-5 mL of 10% buffered formalin. All eggs in each sample were counted under a compound microscope; the number of fertilized and unfertilized eggs was recorded and then analysed with a Likelihood Ratio Chi-square test. Eggs were considered fertilized if a fertilization envelope was present.

4.3.2. Results

In the experiment with *Ulva intestinalis*, the level of successful urchin fertilization in the exudate treatment was significantly lower than the control treatment (Chi-square, $\chi^2 = 14.9$, 1 df, $P<0.001$): there were disproportionately fewer fertilized eggs in the presence of algal exudate (Fig. 8) than in the filtered sweater control. However, in the experiment with *Codium vermilara*, the extent of fertilization did not differ between the exudate treatment and the control ($\chi^2=2.6$, 1 df, $P=0.109$). Thus, the ephemeral macroalga disrupted urchin fertilization success whereas the proliferating perennial *C. vermilara* did not.

4.3.3. Conclusions

Our results provide definitive evidence that ulvoid exudates reduce fertilization (Fig. 8) and, thus, purple urchin production although we have no direct information about environmentally relevant concentrations in the lough. Based on the study by Vázquez et al. (2017), we assume that the mechanism is disruption of the fertilization membrane rather than reduced viability of gametes.

In recent years, there has been a proliferation of ulvoids, ectocarpoids, and other ephemeral macroalgae in Lough Hyne from March through October (Little et al., 2018) and in other Irish coastal waters (Lyons et al., 2014), presumably due to a significant increase in nitrogen (Jessopp, 2011; Jessopp et al., 2011; McAllen, *unpubl. data*). This proliferation is indicative of a bottom-up effect, not a top-down effect that would be expected from a trophic cascade. The recruitment failure of urchins from 2011 to the present was markedly different from the pattern of recruitment seen in 1994–2010 (Trowbridge et al., 2011) and coincided with the domination of ephemeral macroalgae.

A variety of other chemicals (including rare heavy metals, pollutants, etc.) in terrestrial runoff also significantly interfere with *P. lividus* reproduction and development (e.g. Oral et al., 2017). These chemicals should also be assessed in Lough Hyne and other semi-enclosed loughs and bays to determine if they were abundant enough to have contributed to the urchin decline.

4.4. Low-larval availability hypothesis

4.4.1. Methods

Echinopluteus larval duration in *Paracentrotus lividus* is about 3-4 weeks (Boudouresque and Verlaque, 2013) although it may be shorter if unlimited planktonic food is available. Based on the published spawning periods for Ireland (January - March and August - September: Crapp and Willis, 1975; May - July and June - July: Byrne, 1990) and elsewhere (spring and summer, Boudouresque and Verlaque, 2013), we postulated there would be larvae in Lough Hyne in mid to late summer. Past spawning observations at Lough Hyne have included 10 mass spawnings of *P. lividus* in July, 3 in August, and 1 in September (Minchin, 1992). Crook (2003) reported July to September spawning in urchins held in flow-through aquaria at the lough. Furthermore, the zooplankton study by Greenwood et al. (2000) reported that echinoid larvae were present from May through to September in the lough with a peak in July and a secondary peak of late-stage larvae in September. They presumed these were *Paracentrotus* larvae based on their own observations of urchins spawning in July (Greenwood et al., 2000) and July - September (Minchin, 1992).

To determine if Lough Hyne purple urchins were fertile and both sexes were present, we examined 3 adult *Paracentrotus* from the west shore in August 2012; we induced spawning, following methods presents above (section 6.1), and examined the colour and relative abundance of gametes. Although it would have been ideal to sample more urchins, we considered disturbing additional specimens would not be appropriate, given the conservation objectives of the marine reserve.

To evaluate the availability of urchin larvae, we performed extensive plankton tows (typically every 2-3 days) along the western and southern shore of the lough in August and September of 2012, 2013, and 2014. We used a 130-µm mesh net (50 cm diameter) to sample surface waters where Greenwood et al. (2001) found the most larval echinoids. Plankton samples were sieved and examined directly. Echinopluteus larvae were collected and photographed.

On 31 August 2012, we completed a series of 3 horizontal tows from Renouf sector S12/13 to S4, S4 to S1 (mouth of the Goleen), and from W24/23 to W18/19 (Fig. 1). On 4 September 2012, we performed two additional horizontal tows on the west and south shores as well as a vertical tow in the north basin. In August - September 2013, a total of 19 separate tows were performed, following the same four paths: two along the west shore (W12/13–W18 and W18–W22/23) and two along the south shore (W38–S4 and S5–S14/15) (Fig. 1B). In August - September 2014, we made an additional 15 horizontal tows on the western and southern shore of the lough. Thus, we made a total of 40 tows over three years during late summer.

For all tows, the plankton net was pulled behind the University College Cork inflatable RIB at about 1 knot (1.852 km h^{-1}) for 5 min. At the end of each tow, the net was pulled out of the water and the plankton rinsed down into the end. The concentrated contents of the plankton net bottle were poured into a 200-mL bottle, alternating between rinsing and pouring in order to collect all of the plankton. The net was cleaned without the cod end attached between each tow to eliminate inter-tow contamination. The plankton sample was split into five sub-samples of 10 mL each, using a Hensen Stempol pipette. We placed each sample into a zooplankton counting tray, and used a dissection microscope to sort and count the plankton.

To supplement these plankton data, a series of recruitment experiments was conducted in 2012-2018 to eliminate the possibility that the window of larval seasonality had been missed. ‘Welcome mats’ and ‘scrub brushes’ —used by juvenile urchin collectors in the Mediterranean populations of *P. lividus* (Hereu et al., 2004; Tomas et al., 2004; Prado et al., 2009)—were deployed as well as pot-scrubbers and acrylic plates as settlement substrata.

Collectors were deployed in multiple blocks with a minimum of 4-5 collectors per block. They were positioned around the south basin for 2 weeks to 5 months, retrieved, manually defaunated, and quantified. Inter-annual variation in urchin recruitment was expected based on other studies (Hereu et al., 2004; Tomas et al., 2004; Boudouresque and Verlaque, 2013). Reported survival of settling urchins to 2–3 mm (test diameter) was <10% (Azzolina and Willsie, 1987) or 0.5–0.7% (López et al., 1998), depending on conditions, location, etc. It was predicted that purple urchin availability and recruitment would be higher in the north basin than the south basin based on results of Greenwood et al. (2001) for many invertebrate species. Furthermore, it was predicted that there would be higher recruitment on the north end of the west shore than the south end due to the prevailing water current pushing larvae northward along the west shore.

4.4.2. Results

In August 2012, both sexes of urchins were present and all 3 specimens sampled were highly fecund. However, in August and September plankton tows, we found no urchin larvae. In 2013 tows, a few echinoids were found: one recently metamorphosed urchin and three 4-armed pluteus larvae along the west shore. However, it was not possible to know definitively if the larvae belonged to the purple urchin *Paracentrotus lividus*, common urchin *Echinus esculentus*, or green urchin *Psammechinus miliaris*. In 2014, an additional 7 pluteus larvae were found out of 15 tows. Overall, in 40 tows during 3 summers, two recently metamorphosed juveniles and 10 larvae were recorded. Thus, there was a paucity of all echinoid larvae in the lough during the period in which they were expected to be present. Based on our annual counts of all three urchin species (Trowbridge and Little, unpubl. data), we posit that larvae would be primarily those of purple urchins.

For the past seven years (2012–2018), no juvenile urchins have been found on numerous settlement collectors in the lough (data not shown due to zero values but 40+ scrub brushes per year). A few (<5) young-of-the-year were found under shallow subtidal rocks each year, either at monitoring sites or other areas in the lough. Thus, there has been minimal urchin recruitment to the adult habitat in the lough since 2010 (Fig. 3-4); two *Paracentrotus* recruits were seen in 2017 at 8 monitoring sites surveyed.

4.4.3. Conclusions

A few echinopluteus larvae were found in the lough surface waters during the 7 years we sampled. Furthermore, of the 3 *Paracentrotus* specimens assessed for fecundity in 2012, all were highly fecund in August and both sexes were present. The Lough Hyne purple urchins, therefore, have the ability to spawn (historically and currently): we observed spawning urchins in June and September 2017. Thus, some external factors must be constraining reproductive stages, including effects on urchin fecundity, fertilization success, and pluteus production and survival. At such low urchin densities, the Allee effect may be one of the primary factors constraining urchin fertilization. Urchin fertilization success is greatest in aggregations; if urchin densities are too low and/or individuals are too distant, fertilization success is likely to be low. Furthermore, urchin recruitment is frequently positively correlated with adult density (e.g., Ouréns et al., 2014 for *P. lividus* on Atlantic shores and Miller et al., 2007 for *Diadema antillarum* on Caribbean shores). Additional research should be focused on these vulnerable stages to evaluate whether Lough Hyne and Irish purple urchins can recover to form self-sustaining populations.

Because urchin recruitment can often be highly episodic (e.g., Ebert, 1982; Pearse and Hines, 1987), our two-decade study may have missed recruitment pulses with longer periodicities. There are known long-term cycles (e.g., North Atlantic Multidecadal Oscillation, North Atlantic Oscillation, and Russell Cycle) in sea surface temperature and currents in the NE Atlantic Ocean (e.g., Cushing and Dickson, 1976; Garcia-Soto and Pingree, 2012) but evaluating their potential causal role in the supply of pluteus larvae (or lack thereof) to Lough Hyne was beyond the scope of our study, particularly given the absence of long-term monitoring of purple urchin populations around Ireland.

4.5. High post-settlement predation hypothesis

4.5.1. Methods

To evaluate direct predation on juvenile stages of purple urchins, in 2016 young-of-the-year and one-year-old urchins were obtained from John Chamberlain at Dunmanus Seafoods for use in laboratory experiments. In the first trial, 10 urchins (1.0–3.4 mm test diameter) were placed per Petri dish with a freshly collected juvenile spiny starfish (*Marthasterias glacialis*) from the south shore; half the 10 dishes had small starfish (4–5 mm centre of disc to tip of longest ray) and the other half had larger ones (15–18 mm). Urchin survival was monitored every day. Extreme care was taken to ensure that no urchins or seawater associated with the urchins entered Lough Hyne due to marine reserve conservation issues. We also monitored the abundance of *M. glacialis* under rocks at the monitoring sites (Fig. 1B) from 1990 to 2016 together with experimental substrata on the western shore in August – September 2016 and 2017.

4.5.2. Results

Marthasterias glacialis

Although there are many potential predators of purple urchins in the lough (starfish, crabs, and fishes), the only species for which we have direct evidence for a predator increase in the same habitat as the urchins was the spiny starfish. Urchins and spiny starfish abundances were inversely correlated across the 10 sites and 21 years (Spearman’s rank correlation, $r_s=-0.343$, $n=210$, $P<0.001$). There were large fluctuations in recorded numbers of this starfish at the monitoring sites from year to year but there was generally a cyclical pattern until 2015–16 (Fig. 9). Maximum numbers occurred at the SE Labhra monitoring site (140 starfish) in 2004. However, in 2007 we recorded only 2 individuals at this site. By 2008 overall starfish numbers had risen to 58. The trend at several sites was of an increase in starfish from very low numbers in the mid-1990s to a peak in the early 2000s, followed by an extreme reduction by 2014. However, 2015 and 2016 were population-boom years for starfish settlement and growth at the monitoring sites (Fig. 9, Trowbridge et al., 2018) and also on deployed experimental substrata. Most of the starfish located on and under shallow subtidal rocks were <60 mm arm length with modal size of 20-25 mm.

Do starfish actually consume juvenile urchins? Based on our 2016 experiments, the young-of-the-year starfish (4.4 mm from centre of disc to tip of longest ray) do not consume the young-of-the year urchins (1–4 mm test diameter). However, slightly larger starfish (16.2 mm)—presumed to be the 2015 recruits—were able to ingest healthy, hatchery-raised *P. lividus*, leaving intact empty tests (without spines). Most of the urchins consumed were small (1–3 mm). Starfish predation on juvenile stages of urchin could have contributed to the paucity of recruiting urchins (Fig. 3-4). Extensive recent research in the Mediterranean has demonstrated that *M. glacialis* does consume purple urchins, adults and juveniles (Guidetti, 2004; Bonaviri et al., 2009; Galasso et al., 2015; Gianguzza et al., 2016). Spiny starfish studies conducted in Ireland and Portugal (Verlag et al., 2003; Tuya and Duarte, 2012) also support the occurrence of such asteroid predation although the ecological significance of it was not entirely clear.

Asterias rubens

Numbers of this ‘common’ starfish noted during the annual under-rock surveys were usually lower than those of *Marthasterias*, and never reached high levels in two decades of sampling. Overall totals across sites were very low from 2006 to 2011, ranging from 4 to 40. From 2012 to 2014, none were found in the monitoring sectors. All individuals were small juveniles not capable of predating on adult purple urchins although they may have consumed juveniles.

4.5.3. Conclusions

Predation by the growing population of spiny starfish in the shallow subtidal habitat could have caused a total recruitment failure of urchins (if there were any metamorphosing urchins settling). Verling et al. (2003) stated that shallow-water starfish were trophically opportunistic but did consume purple urchins on the north shore of Lough Hyne. Guidetti (2004) reported that 18 species of fishes in 6 families, including sparid and labrid fishes, consumed purple urchins in SW Italy. Furthermore, Bonaviri et al. (2009) reported that predation by *Marthasterias* was a major source of urchin mortality in the marine reserve on Ustica Island, SW Italy. *Marthasterias* ate significantly more female than male *Paracentrotus* in a laboratory experiment and presumably caused the male-skewed sex ratio at Ustica Island (Gianguzza et al., 2009). We present compelling, though indirect, evidence that starfish could have been a significant contributory factor in the urchin decline around the lough. From our own observations, starfish stomach acid weakens the inter-ossicle joints in urchin tests, rendering them extremely fragile. Thus, starfish feeding may leave few persisting urchin tests which collapse down to the component ossicles.

Crab predation would not sufficiently explain our urchin population results (Fig. 3, 5). High crab densities reported by O'Sullivan and Emmerson (2011) did not persist (Matthams, 2015) and few broken tests (indicative of crustacean feeding: Boudouresque and Verlaque, 2013) were seen during our extensive snorkel surveys. Crab abundances fluctuated in relation to parasite-host cycles (Matthams, 2015) and not necessarily to marine conservation policies. Poaching of crabs and lobsters may be important influences on subsequent predation levels. Although such poaching was frequently observed by the first four authors, we have no evidence concerning the scale of such activities.

Even if crab or starfish predation pressure were higher in recent years than before 1981, we strongly refute the suggestion by O'Sullivan and Emmerson (2011) that marine reserve designation was the driving factor for several reasons. There is no evidence (scientific or local knowledge) that fishing pressure was ever intense on the lough, even before 1981. In addition, there were no pre- and post-1981 surveys of predators that were free of the confounding factors such as severe winters of 1978/1979, 1985, 1989 (Trowbridge et al., 2013) and harmful algal blooms of dinoflagellates near the lough (and probably in the lough) in 1978 and 1979 (O'Sullivan, 1978; Cross and Southgate, 1980; Ottway et al., 1980; Pybus, 1980; Southgate et al., 1984). While there may have been a trophic shift and/or a trophic cascade, we do not agree that the Irish marine conservation efforts were to blame.

Human removal of urchins (either for consumptive or scientific purposes) remains a strongly persuasive mechanism of urchin demise. Our review of scientists' collection accounts from the North Wall (e.g. Crook et al., 1999; Crook 2003) could contribute to some of the 'missing' urchins. However, the researchers stated they returned the urchins to the same habitat which would indicate the tests should have been present even if the urchins were in poor condition. Human 'poaching' for food and/or for nursery stock is a much more convincing explanation. It would account for the between-site variation in urchin declines (Fig. 3) and the temporal variation between the decline at our monitoring sites and at the, much more accessible, north shore populations (Fig. 2A vs. 2D). We have certainly seen, first-hand, the poaching of crabs, lobsters, snails, and mussels during the day as well as numerous clandestine scuba divers accessing the lough from the north shore or Goleen at night.

4.6. High post-settlement mortality hypothesis

4.6.1. Methods

Mortality of benthic stages could also be due to abiotic factors. Extreme dissolved oxygen (DO) conditions (hyperoxia and hypoxia) could be lethal to benthic stages of urchins. To quantify DO levels, HOBO data loggers were deployed in 5 different locations in the shallow subtidal areas of the lough (North Labhra, Westwood South, SE Labhra, Sector S1 at the mouth of the Goleen, and Westwood North) where urchins had occurred historically. Data loggers recorded every 15 minutes from early June to September 2017. The duration that DO levels were continuously hypoxic (<2 mg L^{-1}) or suboxic (<6 mg L^{-1}) was calculated for each location and results pooled as the frequency of continuous exposure to hypoxic or suboxic conditions.

To evaluate how low DO levels affected *Paracentrotus lividus*, a series of 1-day experiments were conducted in 2016 and 2017 with urchins of test diameter of 1-4 mm and 8-10 mm obtained from John Chamberlain's Dunmanus Seafoods in Durrus, Co. Cork. One-litre jars of seawater were placed in a cold-water bath using seawater from the lough and compressed nitrogen gas was bubbled into them to set a particular DO concentration in each jar. Using a YSI oxygen probe, nitrogen gas was added until the probe read the desired oxygen concentration.

In the first trial of 2016, 5 DO treatments (8.2, 4.0, 2.9, 1.0, 0.17 mg L^{-1}) were established, ranging from normoxic to low hypoxic with 2 replicate jars per treatment. Ten small urchins were added for 1 day; they were then removed and examined to determine whether they were alive and if so, the movement of their spines, podia, and pedicellariae were noted. In the second trial, 9 urchins (1 year olds) were added to each jar and set up 4 DO level treatments (8.1, 2.0, 1.0, 0.2 mg L^{-1}) with 2 replicates per treatment. In the third trial, 7 urchins (1 year olds) were used per jar, set up 2 DO treatments (normoxic 8.7 vs hypoxic 0.17 mg L^{-1}), and had 3 replicates per treatment. In all cases, after 1 day the seawater was replaced with normoxic water and the urchins that recovered (based on spine, podia, and pedicellariae movements) or died were noted. For all experiments, urchin survival was predicted to be low under suboxic to hypoxic conditions, relative to normoxic controls (~8-9 mg L^{-1}).

In 2017, three additional trials were conducted. In the first, urchin survival and performance were compared in normoxic vs. low hypoxic conditions as well as in Lough Hyne seawater vs. Dunmanus Seafoods seawater (n= 4 replicates of this two-way factorial design). In the second experiment, there were 4 dissolved oxygen treatments (normoxia, suboxia, hypoxia, and low hypoxia: see Table 1) with 5 replicates per treatment. In the final experiment, the time of exposure to low-hypoxic seawater (<0.2 mg L^{-1}) varied: 0, 4, 8, and 10 hours; the duration of the 24-hour experiment was in full normoxic seawater (24, 20, 16, and 14 hours, respectively).

4.6.2. Results

In the 2016 DO laboratory experiments, after 1-day exposure to 0.2 mg L^{-1} seawater, 10 (100%) of the young-of-the-year urchins were dead in one replicate and 5 (50%) in the other. After the 1-day 'recovery' period in normoxic seawater, 2 of the remaining urchins were dead. In the 2017 trial, 6 individuals (33%) were dead in the low DO treatment, 56% were not attached to the substrata and 11% were only loosely attached; in the normoxic treatment, all were firmly attached with their podia to the sides of the glass jars. After the 1-d 'recovery' period, 9 of 21 (43%) urchins were dead in the 0.16 mg L^{-1}

seawater. These results collectively demonstrate that even 1-d exposures of hypoxic (<2 mg L^{-1}) seawater was lethal or sublethal to juvenile urchins. In 2017, 1-day exposures to DO values <1 mg L^{-1} were lethal to sublethal to urchins (Fig. 10A). Even 8 to 10-h exposures were lethal to many juvenile urchins (Fig. 10B).

In the summer of 2017, at five sites where urchin recruitment had historically been high, the dissolved oxygen (DO) levels on the benthos (above the rocks) varied from hyperoxia (supersaturation) to anoxia (no oxygen) (Fig. 10A). At two sites (North Labhra and Westwood North, both in the north basin), the dissolved oxygen levels were repeatedly hypoxic to anoxic at night and hyperoxic in daytime (i.e. diel-cycling hypoxia). However, the duration of extreme conditions was brief, with daily fluctuations between the two extreme levels. DO levels under rocks typically were hypoxic and anoxic in the daytime (Fig. 11A). Thus, the duration of the poor conditions would vary from 15 min to 8-10 hours a day above rocks (Fig. 11B) (and presumably 24 hours a day for under rocks). The duration of suboxia ranged up to about 16 hours a day (Fig. 11C). At other sites and in other years (particularly 2014 and 2015), DO conditions were even lower (detailed results to be reported elsewhere, Plowman et al., unpublished data).

4.6.3. Conclusions

Measurements of nitrogen inside and outside the lough (Jessopp et al., 2011; McAllen et al., unpublished data) indicate nutrient enhancement and, consequently, eutrophication in the past decade, presumably due to agricultural runoff regionally in SW Ireland. Whether eutrophication was the driver of urchin mass mortality and/or partially a consequence of it cannot be unequivocally determined.

Given the recent phenomenon of frequent hypoxia and anoxia on the shallow subtidal sea bed of Lough Hyne (Trowbridge et al., 2017a; Plowman et al., unpublished data), on top of and underneath shallow subtidal rocks, mortality of settling juvenile urchins may now be a major cause of the decline of purple urchins in Lough Hyne. Certainly, research by Saco-Alvarez et al. (2010) and this study would indicate that the urchin habitat quality in Lough Hyne is frequently inadequate for urchin persistence. The demise of sponges, bryozoans, and other invertebrates in the lough (Little et al., 2017b; J. Bell, pers. comm.) support the poor-habitat scenario.

Reviews by Vaquer-Sunyer and Duarte (2008), Diaz and Breitburg (2011), and others have reported the significantly increased frequency of hypoxia in marine coastal waters. Thus, what is happening in Lough Hyne with extreme dissolved oxygen fluctuations (Trowbridge et al., 2017a) is a worldwide problem although it may be exacerbated in areas with limited seawater flushing due to coastal configuration. Furthermore, the lethal and sublethal DO levels of invertebrates varied widely among taxa, and mass moralities of several groups occurred at DO values well above the hypoxia/suboxia transition (Vaquer-Sunyer and Duarte, 2008).

4.7. High-pathogens hypothesis

4.7.1. Methods

To estimate pathogen levels within the lough, visual surveys of sea urchins were made during our snorkel surveys by pairs of snorkelers in August/September each year (2006–2017). Data were recorded by Renouf sector without disturbing the benthic habitat. The condition of all urchins found was typically recorded, and photographs were made of any deleterious conditions such as spine loss, lesions, etc. Furthermore, all urchins found under low-shore rocks during the two-decade monitoring at 10 ‘annual sites’ were examined, and any abnormal condition noted.

4.7.2. Results

Unhealthy urchins were frequently observed in the lough (Supplemental Fig. 2). There were three general categories of ailments: (1) partial to total spine loss in live and dead urchins, (2) epidermal lesions, and (3) white coating of urchin surface usually near the base of spines but occasionally extending up individual spines. These issues occurred in *P. lividus* as well as in the ‘common’ urchin *Echinus esculentus* (Fig. 5). Furthermore, juvenile purple urchins obtained from the Dunmanus Hatchery died in <1 week when being held in buckets of aerated seawater from Lough Hyne in September 2016; this was not an experiment so there was no control. Thus, the water quality itself or pathogens in the water may have contributed to urchin stress and/or mortality. In June 2017, urchin survival did not differ significantly when held in Lough Hyne vs. Dunmanus Bay seawater.

4.7.3. Conclusions

Surprisingly little research has focused on the role of pathogens and/or dinoflagellate blooms contributing to urchin mortality in Ireland compared with other regions such as Nova Scotia, the Caribbean, and the Mediterranean Sea. The role of bald-urchin disease or comparable syndromes in the shift from high-density populations of urchins to low-density ones is well established for Mediterranean urchin populations (Boudouresque and Verlaque, 2013) as well as mass mortalities elsewhere (e.g. Girard et al., 2012). In particular, high temperatures are known to facilitate disease outbreaks by increasing pathogens and reducing host resistance in urchins, corals, and many other organisms. Jones and Scheibling (1985) suggested that *Paramoeba* spp. may have been the causative agent in the mass mortality of green urchins (*Strongylocentrotus droebachiensis*) in Nova Scotia. Bacterial agents were implicated in mass mortalities of Caribbean and California urchins. Hagen (1992) reported that population reductions of green urchins in parts of central Norway may have been related to an infestation by the endoparasitic nematode *Echinomermella matsi* or other waterborne agents. Regretfully, these factors have not been investigated for urchins in Lough Hyne.

The paucity of such research in Europe's first and undoubtedly best-studied marine reserve is concerning from a conservation perspective, particularly given that Girard et al. (2012) demonstrated that large urchins were infected significantly more frequently than juveniles: the mortality of *Paracentrotus* large enough to be sexually mature would significantly curtail larval production. Furthermore, the first author's (C.D. Trowbridge) periodic observations of seawater exchange (dumping and replacement) from trucks of imported seafood with lough seawater should be stopped due to the strong probability of point-source introductions of pathogens.

Similarly, the fact that Lough Hyne has not yet been incorporated by the Irish EPA as a regular monitoring site for harmful algal blooms, nutrients, dissolved oxygen, etc. is unfortunate. An EPA-funded study by Jessopp et al. (2011) was a notable exception. SW Ireland, including Lough Hyne, has experienced increased nutrient-enhancement in many catchments and coastal areas (Jessopp, 2011; Jessopp et al., 2011) compared to two decades ago (Johnson and Costello, 2002). Furthermore, starting in the late 1970s, harmful algal blooms (particularly the dinoflagellate *Karenia mikimotoi*) have occurred in western and southern Ireland (O'Sullivan, 1978; Pybus, 1980; O'Boyle et al., 2016). Many of these blooms caused significant mortalities of fishes and/or invertebrates (Cross and Southgate, 1980; Leahy, 1980; Southgate et al., 1984; Silke et al., 2005), particularly in seasonally stratified coastal waters. In particular, Cross and Southgate (1980) reported the loss of spines by *Paracentrotus* and the urchins' departure from rockpool depressions to lie on the bottom of pools. Yet, only two studies have evaluated dinoflagellate populations in Lough Hyne (Johnson and Costello, 2002; Jessopp et al., 2011) and none have evaluated faunal mortalities during/after blooms. There are extensive possibilities for future environmental research in Ireland and the role of coastal configuration on eutrophication, extreme DO fluctuations and biotic mortalities.

Conclusions: multiple stresses and feedback loops

The current situation in the shallow subtidal of Lough Hyne can be represented by a feedback loop (Fig. 12). We suggest that multiple factors including human collection, starfish predation, and declining habitat quality due to coastal eutrophication were all causal factors in urchin population decline. Ephemeral algal growth reduces water movement, allowing algal decay and promoting hypoxic to anoxic conditions. Hypoxia in turn promotes death or stress of adult urchins and reduces larval recruitment. Reduction in the urchin population in turn promotes further growth of filamentous algae. This feedback loop can be accelerated by external influences such as increases in predation level, nutrient supply and the disruptive effects of weather conditions such as storms. Climatic change could exacerbate the interactions in several ways: (1) increasing the frequency or magnitude of toxic algal blooms (e.g., *Karenia* or *Ostreopsis*), pathogen outbreaks, or extreme weather, (2) increasing the seasonal appearance of warm-water triggerfish known to consume urchins, and (3) increased proliferation of the spiny starfish which spawn during warm-water periods (Minchin, 1992). The anthropogenic effect of increased fertilization of Irish coastal pastures will cause continued nutrient enhancement, ephemeral macroalgal proliferation, and, eventually, eutrophication of coastal waters. Without human intervention to improve water quality and replaced lost urchins, it seems unlikely that the situation will change in the near future.

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FIGURE CAPTIONS

Fig. 1. A, Location of Lough Hyne in SW Ireland, showing places mentioned in the text. B, Map of Lough Hyne, showing 10 long-term monitoring sites (10 m wide on shore) that were surveyed annually for 2 weeks in late August to early September for 21 years (‘Annual’ sites), and 10 sites that were surveyed in 2015 to compare with older surveys (‘Historical’ sites). Annual site names are abbreviated as follows: BB, Boundary Bay; CB, Codium Bay; EC, East Castle; EG, East Goleen; GY, Graveyard; NI, North Island; NL, North Labhra; WWN, Westwood North; WWS, Westwood South. Historical site names are abbreviated as follows: BH, Bohane Harbour; GQ, Glan Quay; NC, North Castle; NWC, Northwest Castle; RN, Rookery Nook; SC, South Castle; SL, South Labhra; WC, West Concrete; WL, West Labhra; WP, Whirlpool Point).

Fig. 2. A, Counts of the purple urchin *Paracentrotus lividus* at the 10 monitoring sites showing the population peak in late 1990s. B, urchin counts pooled by basin (north vs. south basin sites). C, Counts of the urchins large enough to be sexually mature (black bars) and small enough to be considered young-of-the year (recent recruits) (grey bars). D, Visible purple urchins (on logarithmic scale) on north shore of lough. Black bars indicate counts based on the road or wall above the shore and grey bars indicate while snorkeling. In 2009 and 2014, there were no visible urchins remaining on north shore.

Fig. 3. Kite diagrams indicating (A) urchin abundance (counts per 10-m long site) from 1994 to 2014 and (B) recruits (urchins < 10 mm test diameter) from 1996 to 2014 at 10 study sites. Site names abbreviated as in caption of Fig. 1. Maximum sample sizes indicated for each kite distribution.

Fig. 4. Size-frequency distributions of test diameters of *Paracentrotus lividus* from 1996 to 2014. Sample sizes indicate the number of measured urchins at 10 monitoring sites. Black bars indicate the young-of-the-year (recruits), hatched bars indicate intermediate-sized urchins, and gray ones indicate potential sexually mature individuals (based on test diameter).

Fig. 5. Number of urchin tests recorded during the shore surveys at the monitoring sites (A-C) and during the whole-lough snorkel surveys (D-F). Mortalities were categorized by year (A, D), site or shoreline (B, E), or apparent cause (C, F).

Fig. 6. Seawater temperatures from various TidBit sensors deployed in the shallow subtidal zone on the western shore since spring 2014. Each panel represents output from multiple sensors downloaded approximately every 6 months; thus, the x-axis scaling varies among panels. Each sensor recorded every

15 minutes during the survey period; the values represent means and standard deviations among sensors. The two summers indicated as cool had extremely negative North Atlantic Oscillation values in July (Trowbridge et al., 2018).

Fig. 7. Late summer surface temperatures measured with a thermometer at Lough Hyne. The Gate Lodge readings were taken offshore from the promontory located in Renouf sector N12; the Glan Lab readings were taken from the quay at the Glannafeen Laboratory, which was at the intersection of sectors S4 and S5. Other includes North Quay, center of north basin, etc. The arrow indicates the 1992 summer which was the only cool summer data recorded.

Fig. 8. Urchin fertilization experiment results with *Ulva intestinalis* in September 2013.

Fig. 9. Temporal changes of spiny starfish (*Marthasterias glacialis*) at 10-m wide monitoring sites in Lough Hyne.

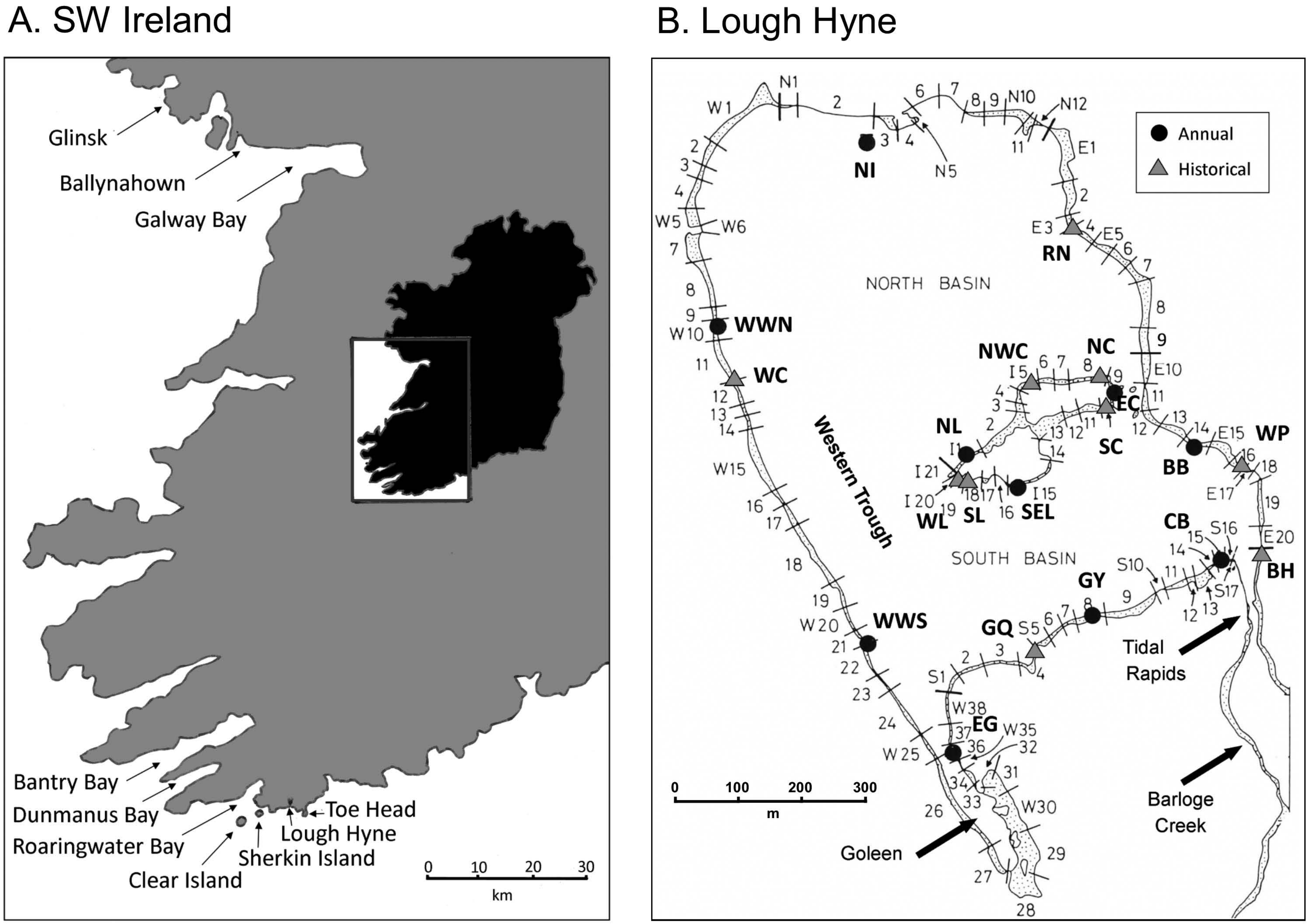
Fig. 10. A, Movement of juvenile purple urchins exposed to varying dissolved oxygen levels for 24 hours in June 2017 at Lough Hyne. Attached indicated the percentage of urchins that were attached to the side of the glass jar; righting refers to the percentage of urchins that could right themselves after being flipped upside down. B, Survival of juvenile urchins exposed to anoxic conditions for 10, 8, or 4 hours vs. normoxic control conditions. Spines, pedicellariae, and podia refer to the percentage of urchins that were moving those body parts at the end of the experiment.

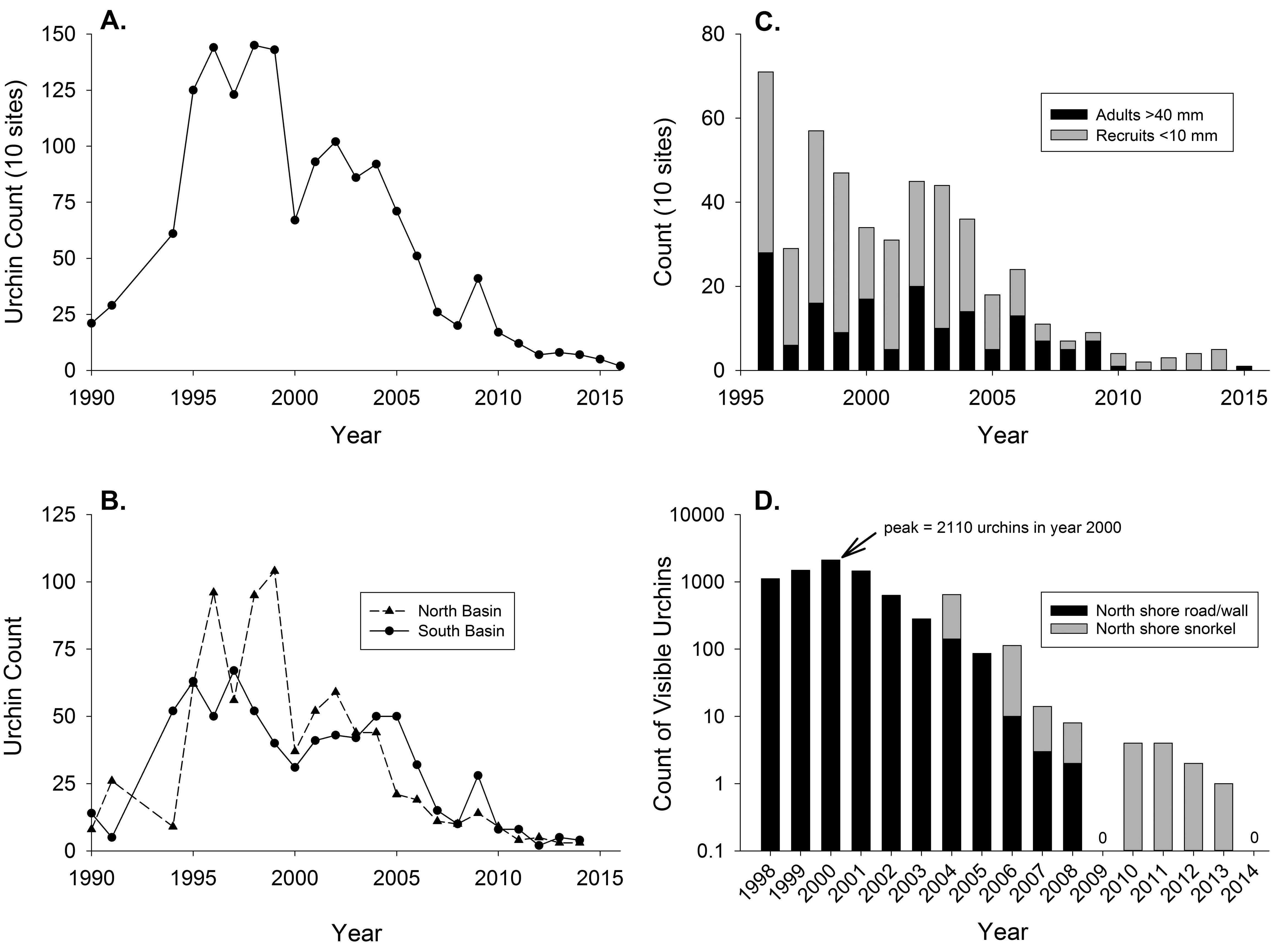
Fig. 11. A, Box and whisker plots of dissolved oxygen values recorded in the shallow subtidal habitats at 5 sites with known past urchin recruitment. Data were recorded every 15 min from June to Sep 2017. Normoxic levels varied between 8 and 10 mg L^{-1} (temperature dependent); hypoxic levels are <2 mg L^{-1}. B, Frequency of DO being <2 mg L^{-1} (hypoxic) vs. duration of time (in 15 min intervals). C, Frequency of DO being <6 mg L^{-1} vs. duration of time (in 15 min intervals).

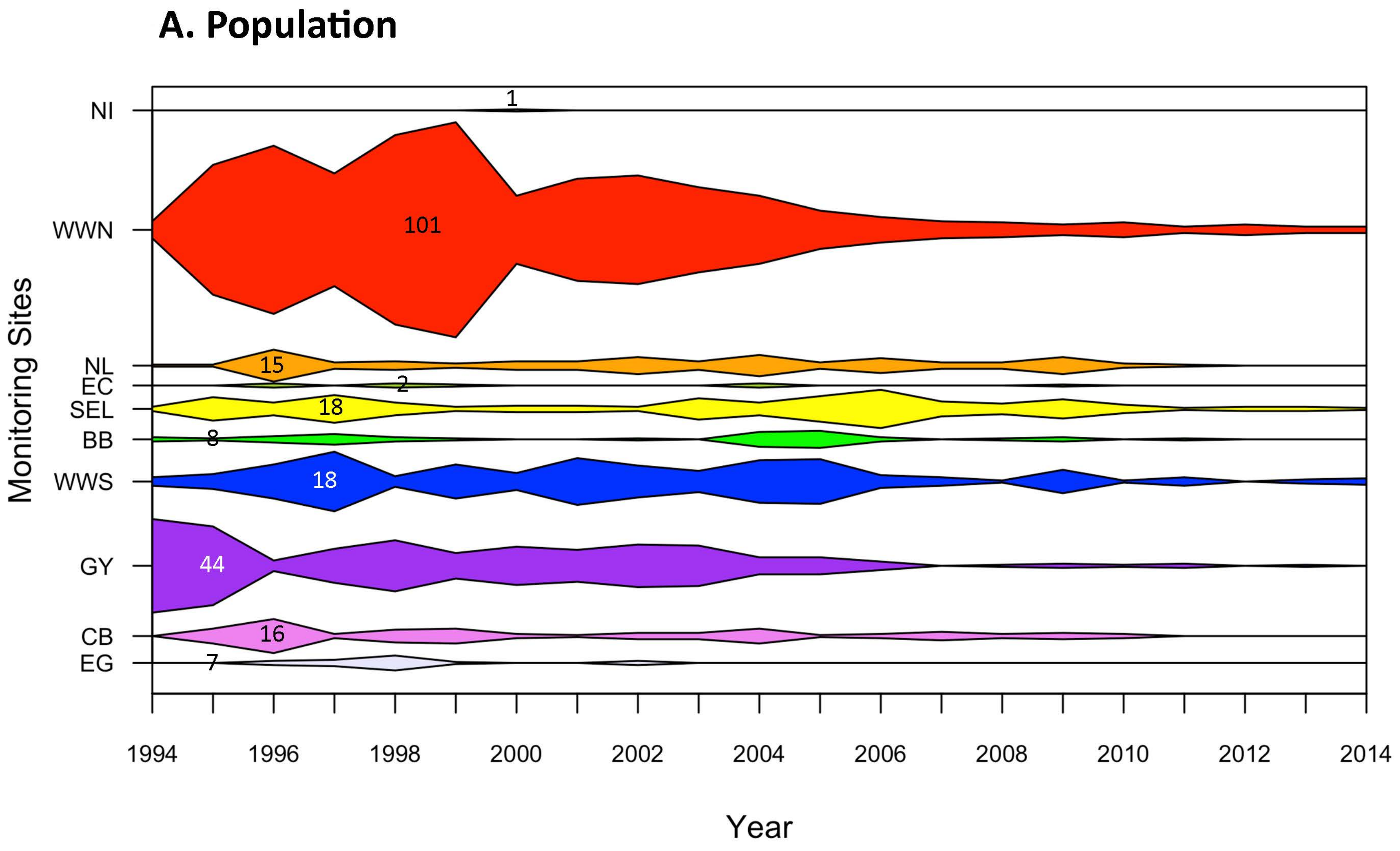
Fig. 12. Schematic feedback loop of interactions in Lough Hyne occurring since 2010.

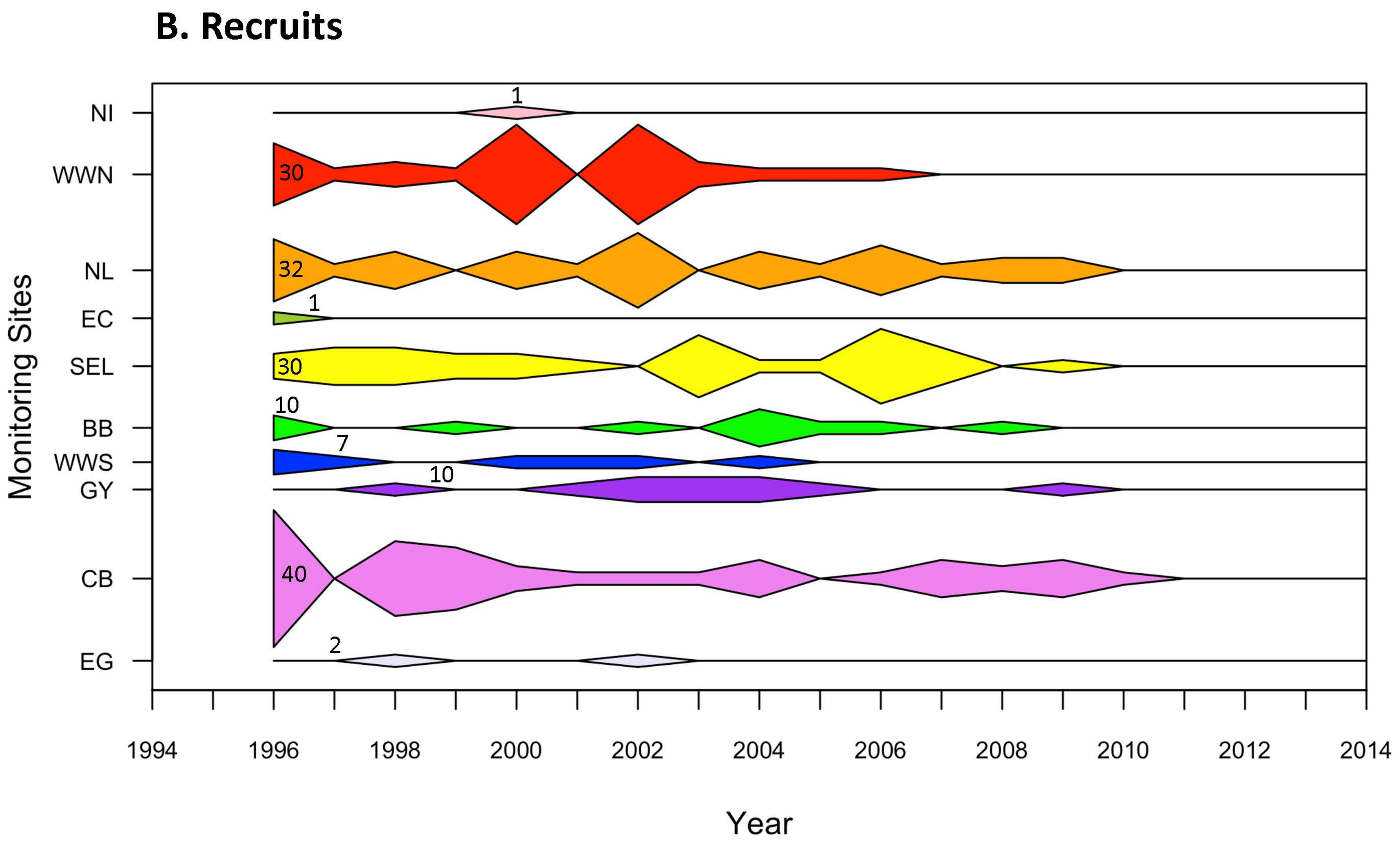
Supplemental Fig. S1. Extreme weather in terms of air temperature from the Sherkin Island recording station. C, Rainfall and D, wind speed at Sherkin. Dashed horizontal lines (A-C) are heuristic tools to draw attention to the circled (A) hot, (B) cold, and (C) wet outlying values.

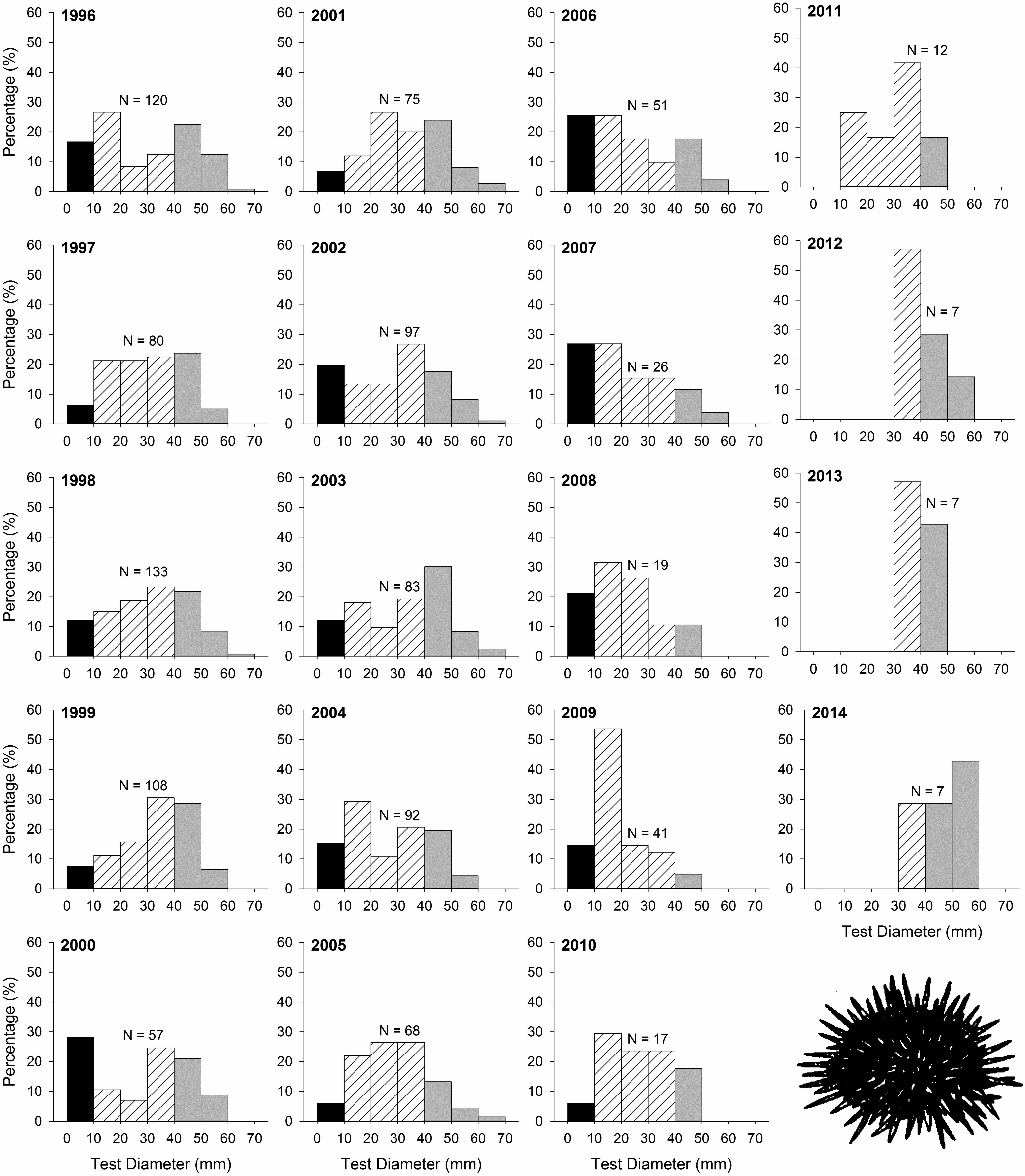
Supplemental Fig. S2. *Paracentrotus lividus* with spine loss (A), spine loss and necrosis (B), and white patches around base of spines (C). The coexisting pink or common urchin *Echinus esculentus* exhibiting similar spine loss.

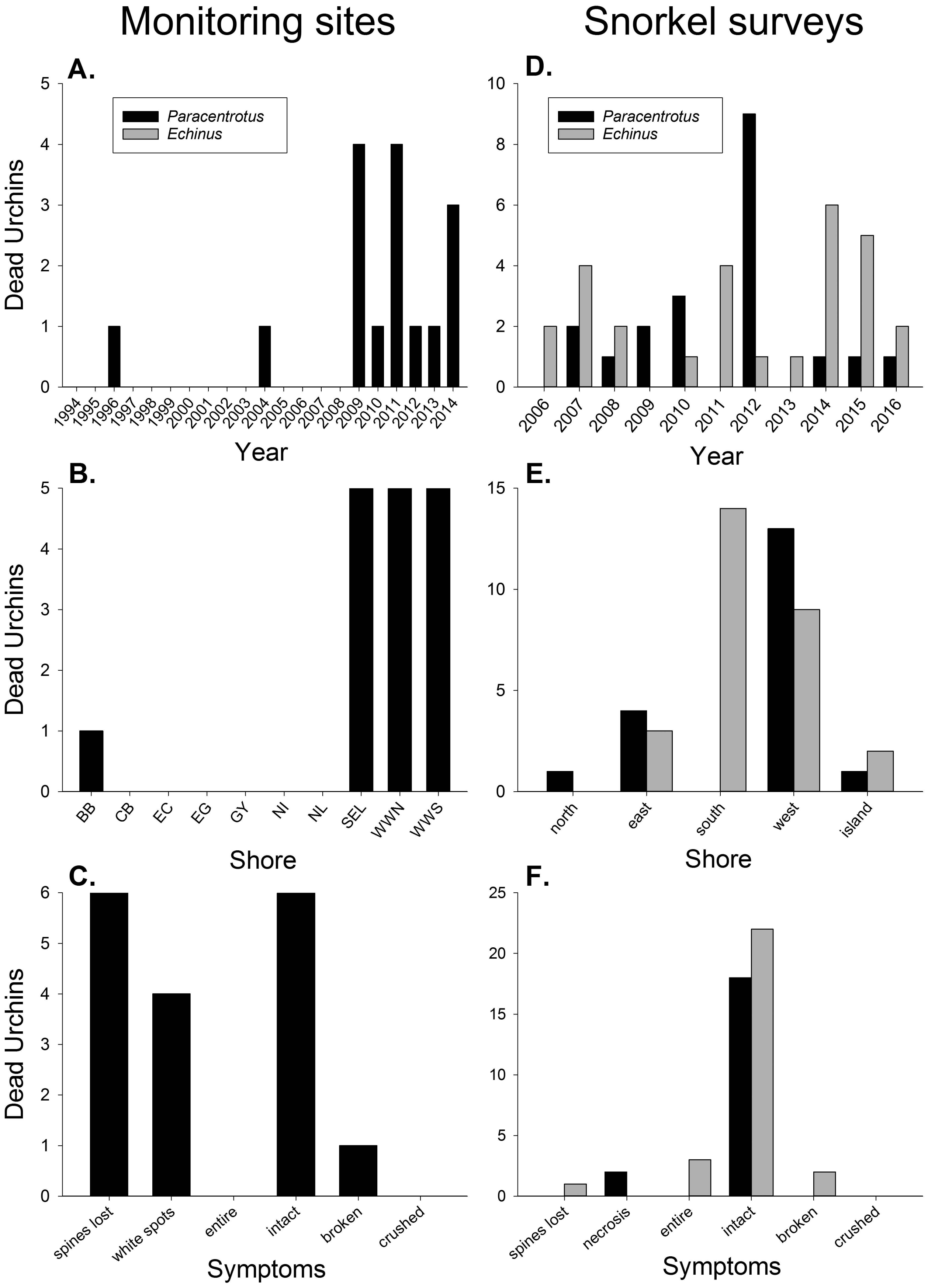

A. SW Ireland
Glinsk
Ballynahown
Galway Bay
Bantry Bay
Dunmanus Bay
Roaringwater Bay
Clear Island
Sherkin Island
Lough Hyne
Toe Head
0
10
20
30
km
B. Lough Hyne
Annual
Historical
NORTH BASIN
SOUTH BASIN
Western Trough
NI
RN
WWN
WC
NWC
NC
EC
SC
NL
WL
SL
SEL
BB
WP
CB
BH
GY
GQ
WWS
EG
Tidal Rapids
Barloge Creek
Goleen
W1
W5
W6
W10
W15
W20
W25
W30
W35
W38
N1
N5
N10
N12
E1
E3
E5
E10
E15
E17
E20
I1
I5
I15
I20
I21
S1
S5
S10
S16
S17
0
100
200
300
m

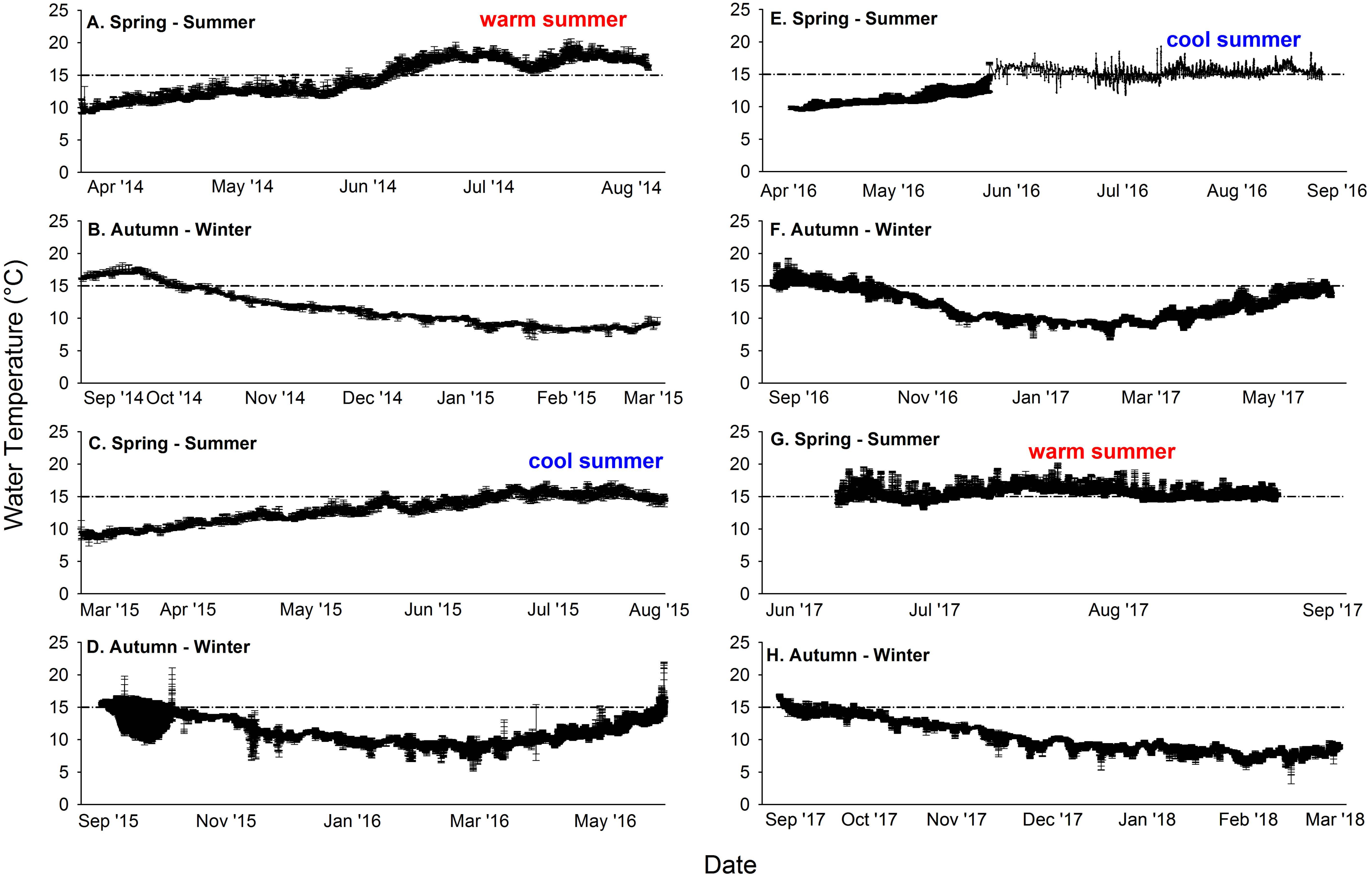

A.
Urchin Count (10 sites)
150
125
100
75
50
25
0
1990
1995
2000
2005
2010
2015
Year
B.
Urchin Count
125
100
75
50
25
0
1990
1995
2000
2005
2010
2015
Year
North Basin
South Basin
C.
Count (10 sites)
80
60
40
20
0
1995
2000
2005
2010
2015
Year
Adults >40 mm
Recruits <10 mm
D.
Count of Visible Urchins
10000
1000
100
10
1
0.1
peak = 2110 urchins in year 2000
North shore road/wall
North shore snorkel
0
0
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
Year


A. Population
NI
WWN
NL
EC
SEL
BB
WWS
GY
CB
EG
Monitoring Sites
1
101
15
2
18
8
18
44
16
7
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year

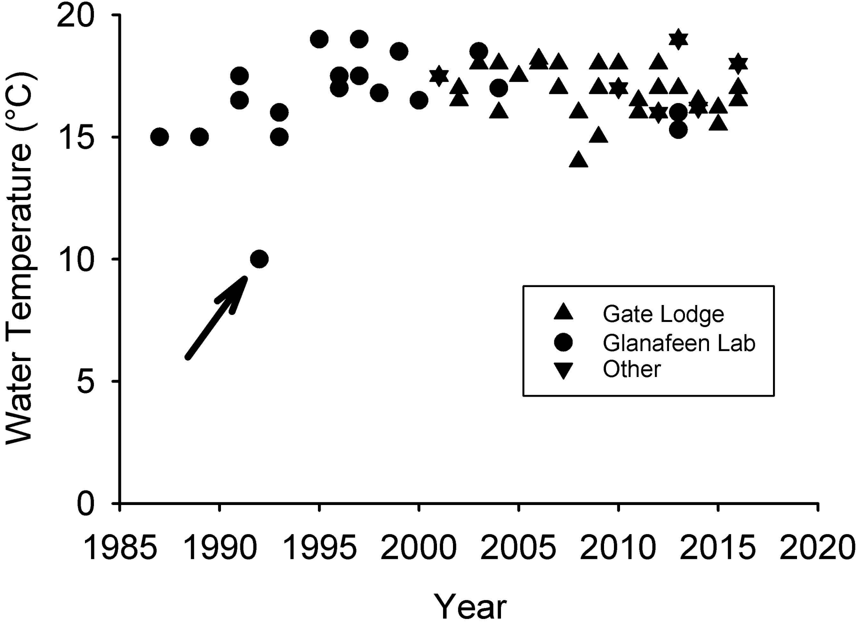

B. Recruits
NI
WWN
NL
EC
SEL
BB
WWS
GY
CB
EG
Monitoring Sites
1
30
32
1
30
10
7
10
40
2
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year

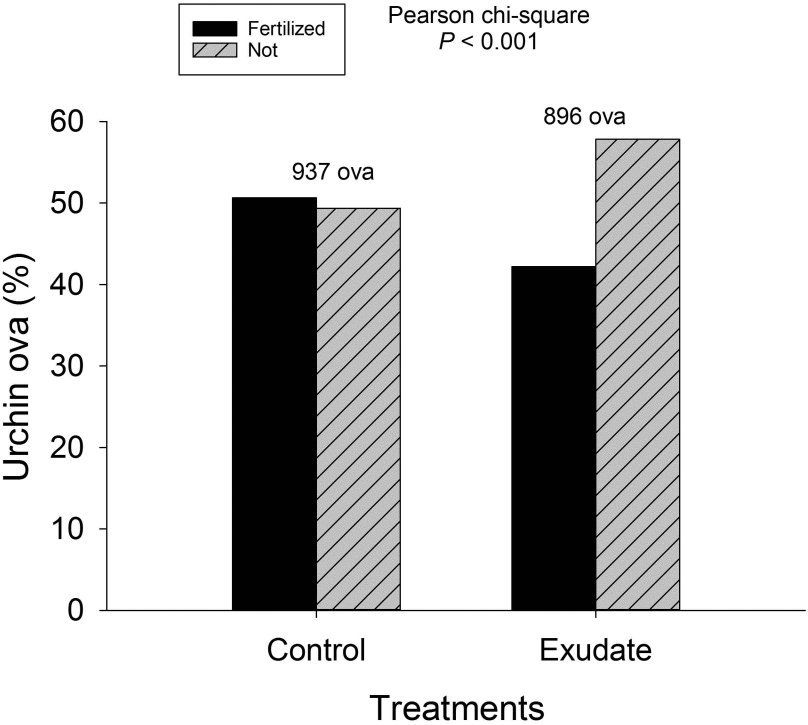

1996
N = 120
2001
N = 75
2006
N = 51
2011
N = 12
1997
N = 80
2002
N = 97
2007
N = 26
2012
N = 7
1998
N = 133
2003
N = 83
2008
N = 19
2013
N = 7
1999
N = 108
2004
N = 92
2009
N = 41
2014
N = 7
2000
N = 57
2005
N = 68
2010
N = 17
Percentage (%)
0
10
20
30
40
50
60
0
10
20
30
40
50
60
70
Test Diameter (mm)


Monitoring sites
Snorkel surveys
A.
Paracentrotus
Echinus
Dead Urchins
0
1
2
3
4
5
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
Year
D.
Paracentrotus
Echinus
0
2
4
6
8
10
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
Year
B.
Dead Urchins
0
1
2
3
4
5
BB
CB
EC
EG
GY
NI
NL
SEL
WWN
WWS
Shore
E.
0
5
10
15
north
east
south
west
island
Shore
C.
Dead Urchins
0
1
2
3
4
5
6
spines lost
white spots
entire
intact
broken
crushed
Symptoms
F.
0
5
10
15
20
25
spines lost
necrosis
entire
intact
broken
crushed
Symptoms

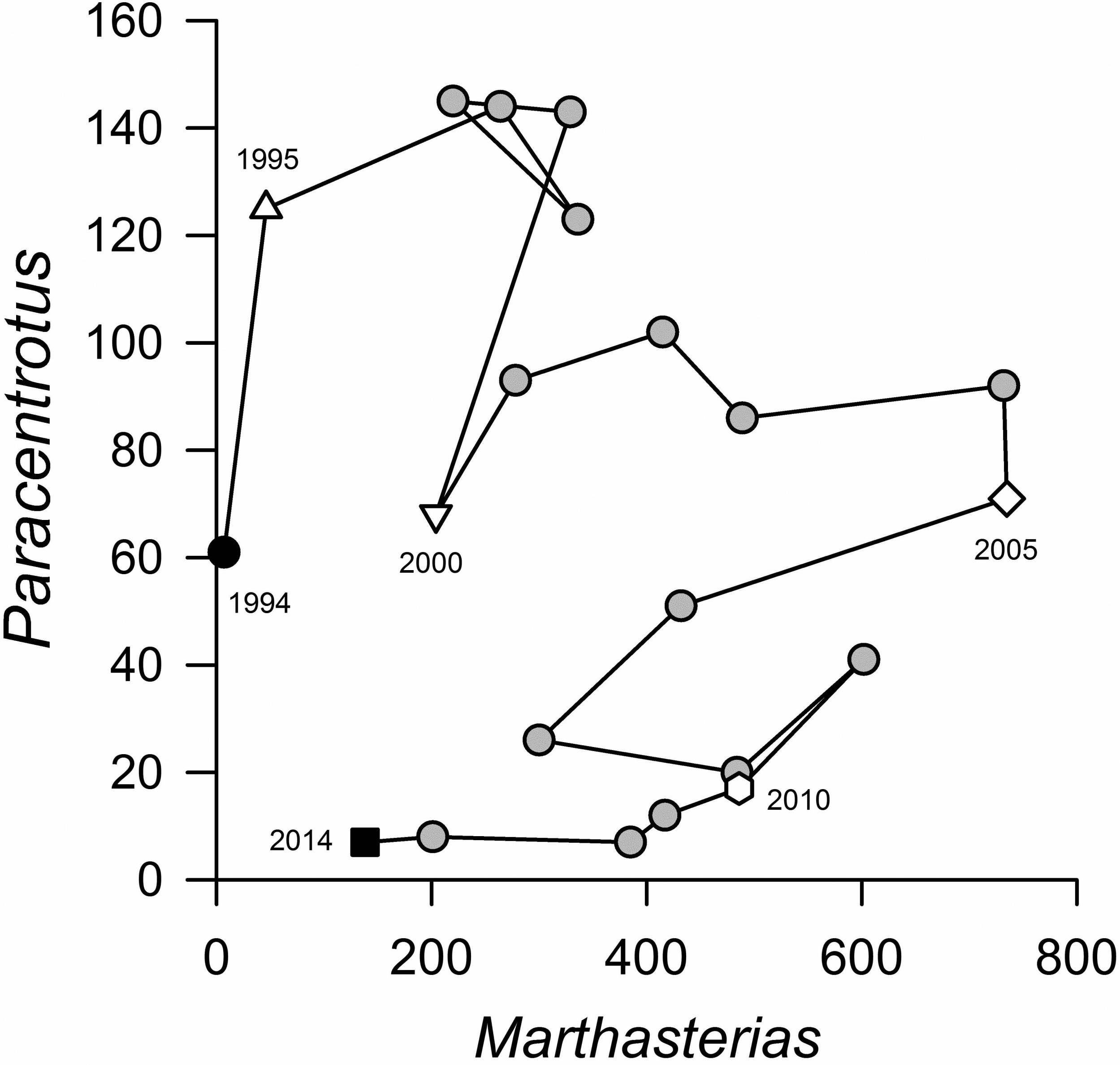


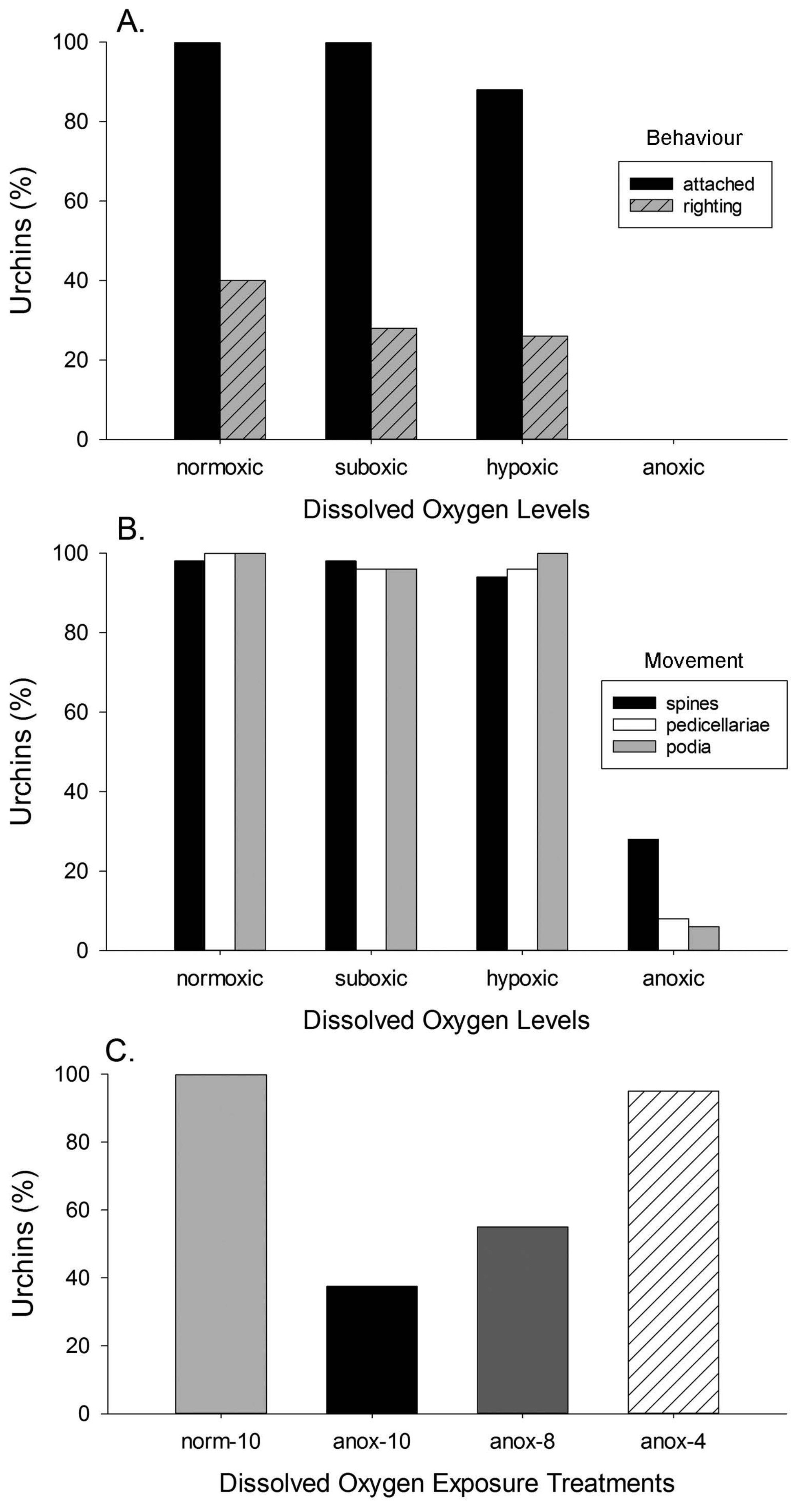
Water Temperature (°C)
Date
A. Spring - Summer
warm summer
Apr '14
May '14
Jun '14
Jul '14
Aug '14
B. Autumn - Winter
Sep '14
Oct '14
Nov '14
Dec '14
Jan '15
Feb '15
Mar '15
C. Spring - Summer
cool summer
Mar '15
Apr '15
May '15
Jun '15
Jul '15
Aug '15
D. Autumn - Winter
Sep '15
Nov '15
Jan '16
Mar '16
May '16
E. Spring - Summer
cool summer
Apr '16
May '16
Jun '16
Jul '16
Aug '16
Sep '16
F. Autumn - Winter
Sep '16
Nov '16
Jan '17
Mar '17
May '17
G. Spring - Summer
warm summer
Jun '17
Jul '17
Aug '17
Sep '17
H. Autumn - Winter
Sep '17
Oct '17
Nov '17
Dec '17
Jan '18
Feb '18
Mar '18
0
5
10
15
20
25

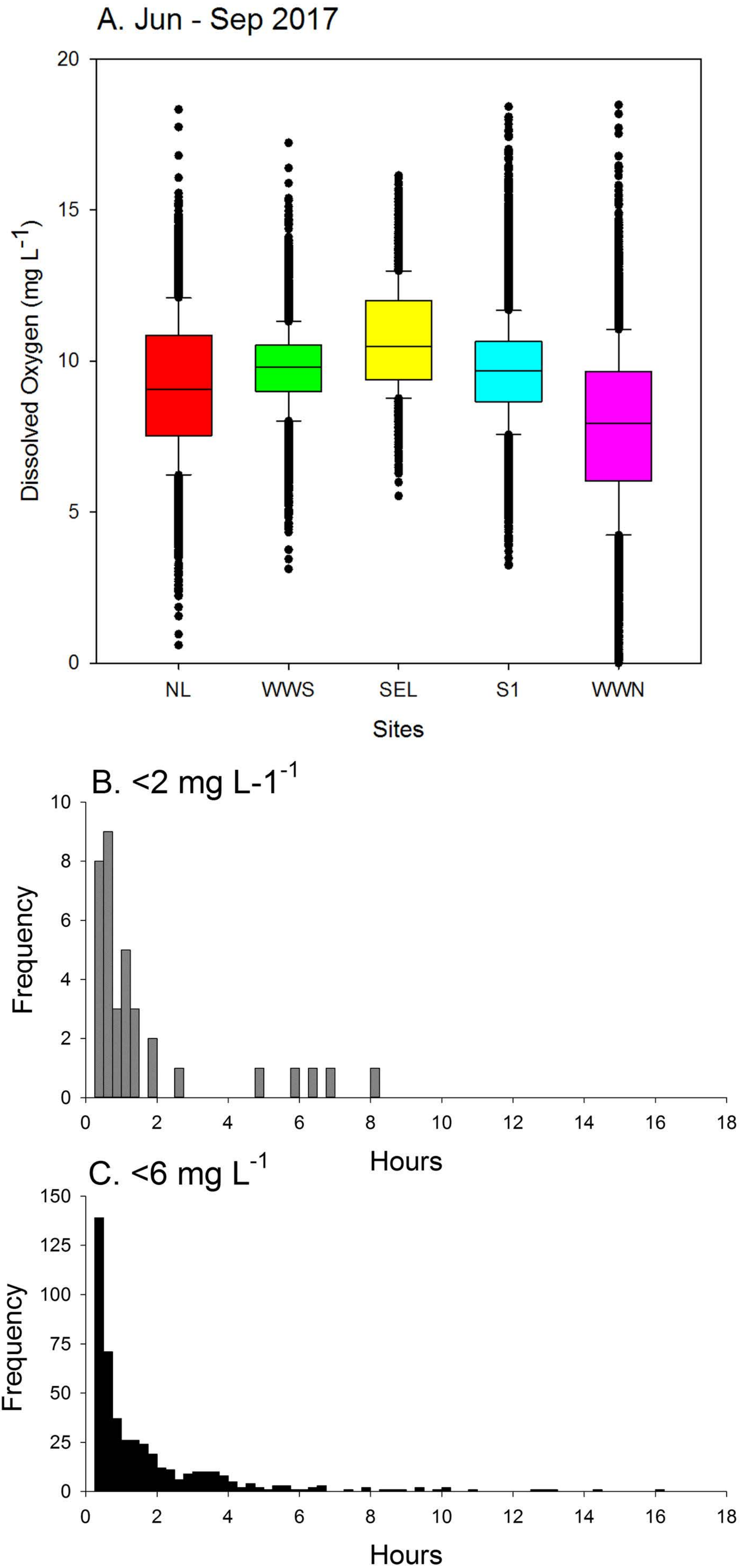

20
15
10
5
0
Water Temperature (°C)
1985
1990
1995
2000
2005
2010
2015
2020
Year
▲ Gate Lodge
● Glanafeen Lab
▼ Other



Fertilized
Not
Pearson chi-square
P < 0.001
60
50
40
30
20
10
0
Urchin ova (%)
937 ova
896 ova
Control
Exudate
Treatments


160
140
120
100
80
60
40
20
0
0
200
400
600
800
Paracentrotus
Marthasterias
1994
1995
2000
2005
2010
2014

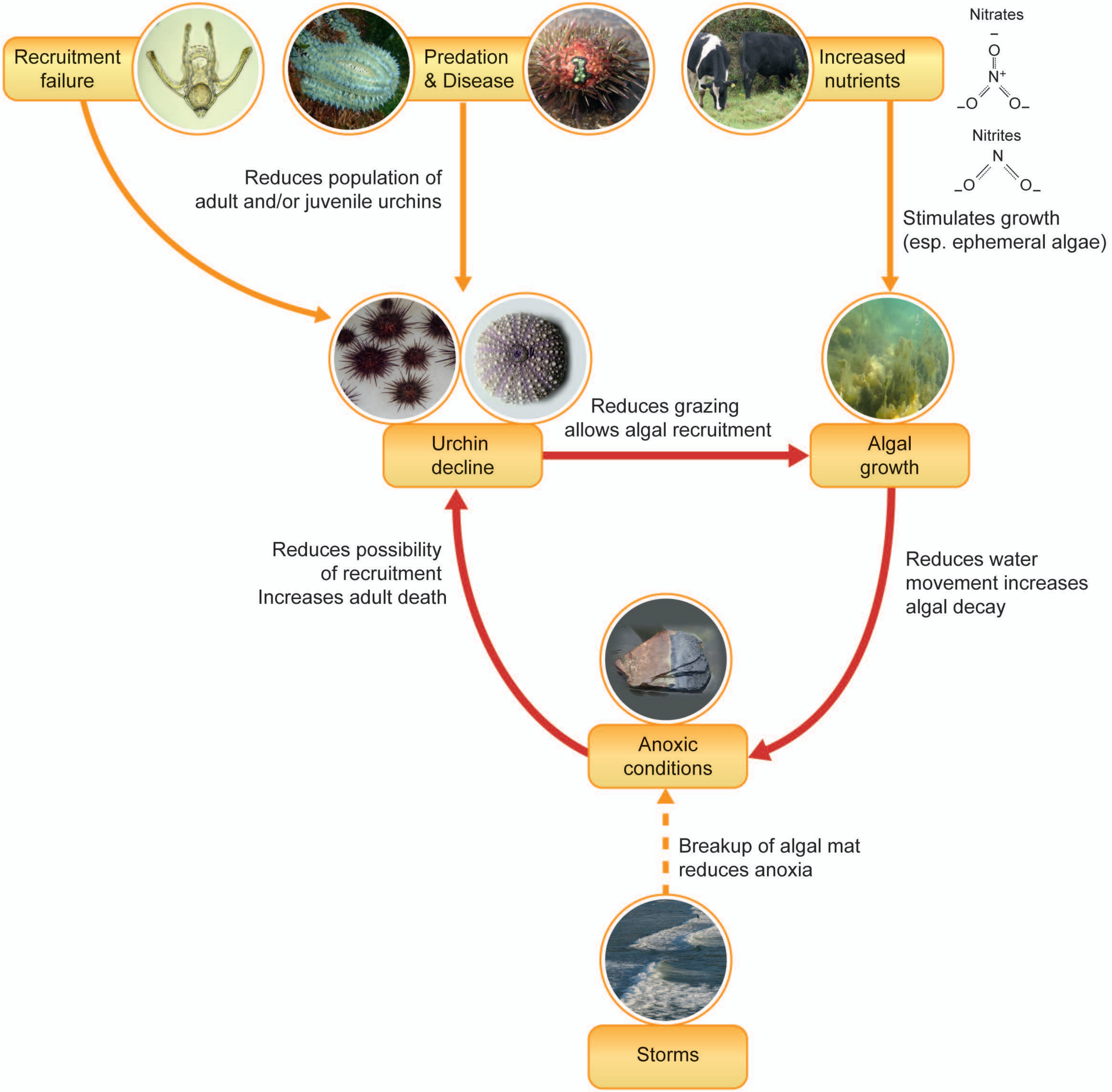
A.
100
80
60
40
20
0
Urchins (%)
Behaviour
attached
righting
normoxic
suboxic
hypoxic
anoxic
Dissolved Oxygen Levels
B.
100
80
60
40
20
0
Urchins (%)
Movement
spines
pedicellariae
podia
normoxic
suboxic
hypoxic
anoxic
Dissolved Oxygen Levels
C.
100
80
60
40
20
0
Urchins (%)
norm-10
anox-10
anox-8
anox-4
Dissolved Oxygen Exposure Treatments

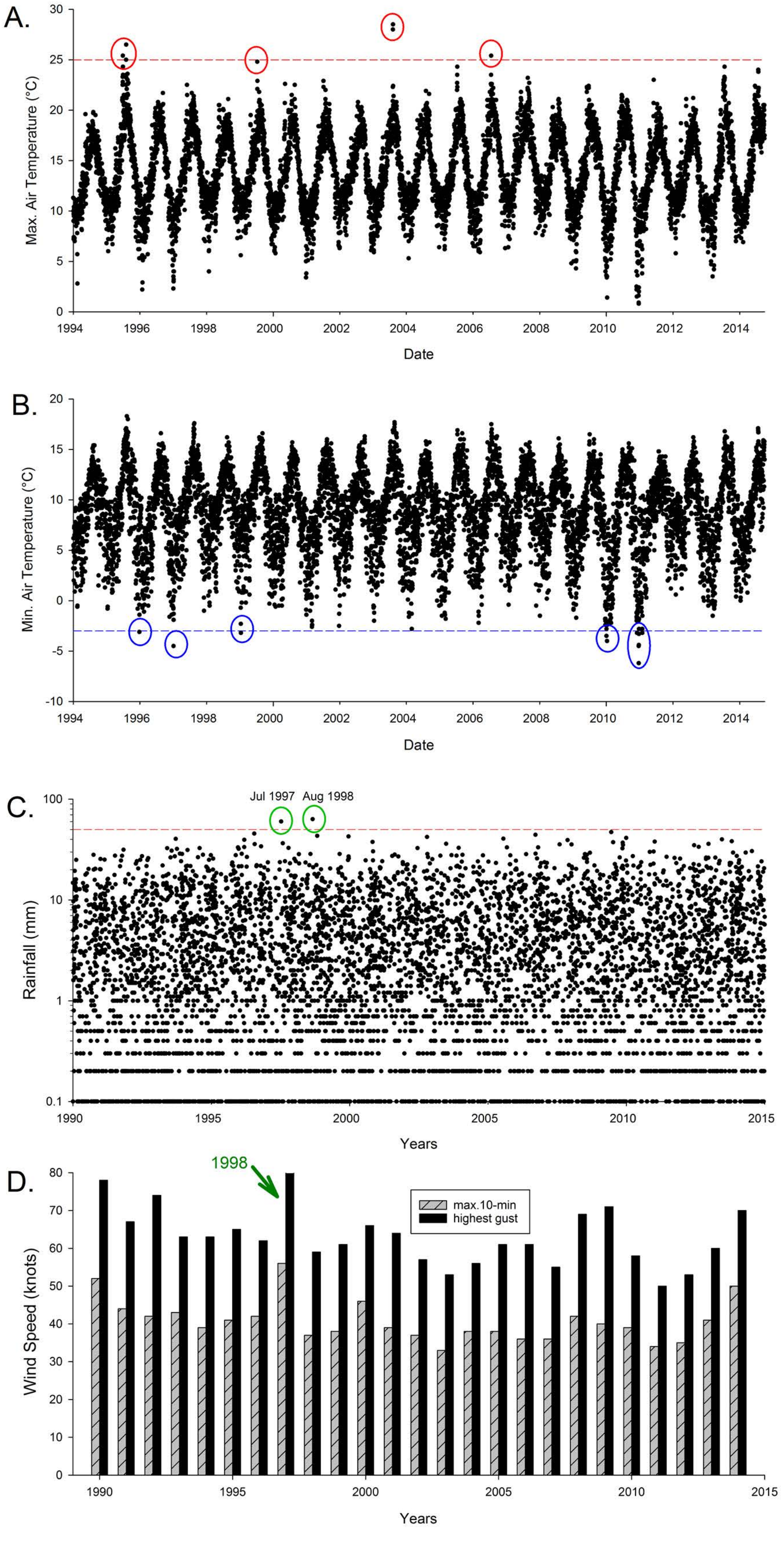


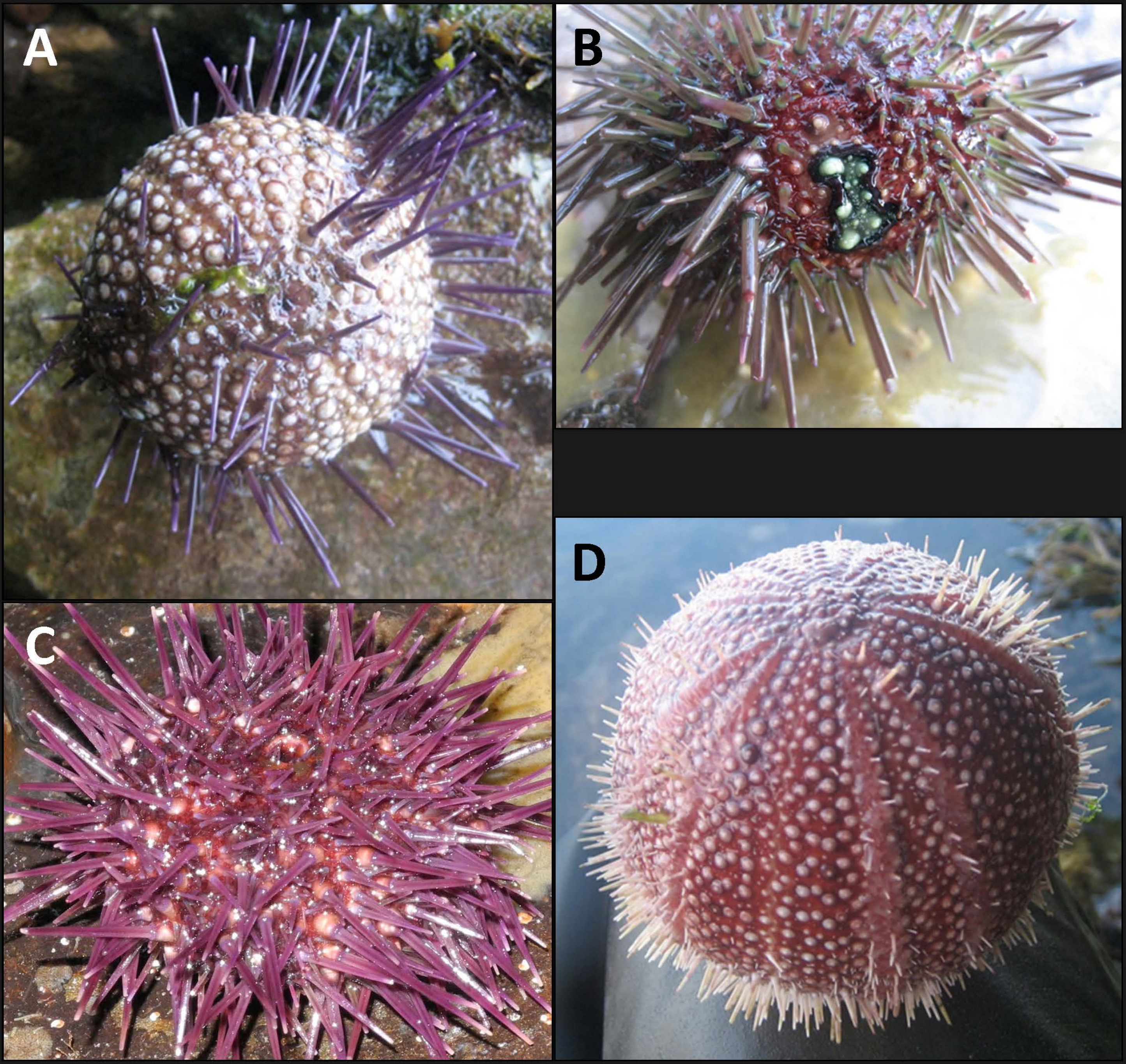
A. Jun - Sep 2017

B. <2 mg L-1^{-1}

C. <6 mg L^{-1}


Recruitment failure
Predation & Disease
Increased nutrients
Nitrates
Nitrites
Reduces population of adult and/or juvenile urchins
Stimulates growth (esp. ephemeral algae)
Urchin decline
Reduces grazing allows algal recruitment
Algal growth
Reduces possibility of recruitment Increases adult death
Reduces water movement increases algal decay
Anoxic conditions
Breakup of algal mat reduces anoxia
Storms


A.
Max. Air Temperature (°C)
0
5
10
15
20
25
30
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Date
B.
Min. Air Temperature (°C)
-10
-5
0
5
10
15
20
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Date
C.
Rainfall (mm)
0.1
1
10
100
Jul 1997
Aug 1998
1990
1995
2000
2005
2010
2015
Years
D.
Wind Speed (knots)
0
10
20
30
40
50
60
70
80
1998
max.10-min
highest gust
1990
1995
2000
2005
2010
2015
Years


A
B
C
D