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Sea temperature variability and *Paracentrotus lividus* (Echinoidea) population fluctuations

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Observations and censi of the echinoid *Paracentrotus lividus* over 40 y at Lough Hyne marine nature reserve have revealed population fluctuations of >4 orders of magnitude. The *P. lividus* population has been anomalously low since the mid 1980s. The population age–size structure has also changed considerably and is now dominated by older individuals. Sea temperature is a known and important determinant of spawning (and recruitment) in this species. In certain years sea surface temperatures (SST) may not reach critical values for *P. lividus* mass-spawning to be triggered. In addition, toxic dinoflagellate blooms may have been responsible for large-scale mortalities within short periods. Years of anomalously low SSTs match the timing of critical decreases in the Lough Hyne *P. lividus* population. Years with low maximum SSTs coincide with the timing of major El Niño Southern Oscillation (ENSO) events. We suggest a SST and possibly ENSO link to unfished (Lough Hyne) *P. lividus* population changes and propose such links as potential aggravating factors in the decline of the fisheries.

The European echinoid *Paracentrotus lividus*, has shown a wide-scale catastrophic decline, through direct over fishing, centred around the country of its biggest destination market, France (Southward & Southward, 1975). At Lough Hyne, Co. Cork (Europe's first designated marine reserve) and much of the Mediterranean Sea it is the dominant grazing species and controls the algal successional series by prevention of space monopolization by superior local competitors (Kitching, 1987). The Lough Hyne population was recorded as alternating between high and low densities since the 1920s (Renouf, 1931; Muntz et al., 1965; Kitching, 1987; Barnes et al., 1999).

Interannual sea surface temperature (SST) variability has been found to positively influence the recruitment of certain fish (Planque & Fox, 1998). One such cause of SST variability on local and global scales is the incidence of El Niño Southern Oscillation (ENSO) events, the collective name for a complex of ocean–atmosphere processes. Oceanographic conditions have been influenced by ENSO events for the majority of the last decade, in contrast to any other decade recorded previously (Glantz, 1996). Typically strong ENSO events influence ocean current strengths and SSTs, both of which have a critical role in mass spawning viability and larval recruitment (Underwood & Fairweather, 1989). Here we link long-term population dynamics in the Lough Hyne *P. lividus* community from the late 1950s to 2000 with SST variation using data from the literature. SST values at Lough Hyne are also compared to the critical spawning temperature of *P. lividus* and the incidence of ENSO events.

Lough Hyne is situated in the south-west corner of Ireland and is thus greatly influenced by the Gulf Stream oceanic current. South Basin observations and summer censuses have been carried out for >40 y. All censuses were made from a row-boat with two observers who counted visible *P. lividus* individuals in the South Basin through perspex viewing-boxes. All individuals between 0 and 3-m depth were easily countable, as surveys are conducted when water clarity >3 m.

The objectives of the present study were to compare databases on *P. lividus* population fluctuations at Lough Hyne with SSTs for local and regional level. We also aimed to compare the timing and duration of ENSO events with SST data and with *P. lividus* population fluctuations. SSTs have been measured in Lough Hyne sporadically from 1965 to 2000 (Kitching, 1987; Minchin, 1992; Ballard & Myers, 1997; this study). Data sets of Irish and North Sea SST were obtained from the literature.

Paracentrotus lividus dominated the shore (with over 200 ind m^{-2}) during early studies at Lough Hyne (Renouf, 1931) but has fluctuated in density since (Figure 1). The timing of critical changes in the Lough Hyne *P. lividus* community has coincided with low maximum SST values at the same locality. From 1965 to 1983 the two lowest SST values corresponded with the start point of the two major declines of the *P. lividus* population at Lough Hyne. The second of the two declines corresponded with a 4-y period when Lough Hyne and Irish Sea SSTs never reached 17°C, the threshold for mass spawning (Fenaux, 1968). Lough Hyne SST values strongly correlated with those of the Irish Sea ($r^2=0.81$; $P<0.01$) but did not relate to North Sea ($r^2=0.02$; $P=0.45$) values. The low SST values in Ireland in the early 1960s, late 1970s and mid 1980s did have similarly corresponding low values for the same periods in the North Sea.

The timing and duration of major ENSO events is shown, together with SSTs, Lough Hyne South Basin population in Figure 2. SST values were below 17°C in three of the 20 non-ENSO influenced years but were less than this critical value in 14 of 18 influenced ENSO years. The average maximum SST reached in a 'non-ENSO' influenced year was 17.5°C, 2.3°C above, and significantly higher (Mann–Whitney *U*-test, $P<0.004$), than a 'typical' ENSO event year (15.2°C). The ENSO events centring around 1967 and 1978 coincided with the two major population decreases at Lough Hyne (Figure 2). The median values of *P. lividus* population change for typical (non-ENSO) years and ENSO event years, +3.2% and −55.9% change respectively, were significantly different (Mann–Whitney *U*-test, $P<0.02$). If ENSO events do (negatively) influence *P. lividus* populations, it would be expected to be through reduced spawning and thus reduce next year's juvenile population.

The *P. lividus* population at Lough Hyne has fluctuated in size by several orders of magnitude over a period of four decades. The compiled evidence up to the mid 1980s suggested that the *P. lividus* population at Lough Hyne might show a similar cyclical nature (10-y duration; see Figure 1 and Barnes et al., 1999) to the American *Strongylocentrotus* populations. This cycle also involved a change of algal dominance to barrens alternation reported from the Pacific and Atlantic coasts of North America (Kitching, 1987). Changes in predator populations have been linked to such fluctuations in echinoids (Elner & Vadas, 1990).

In contrast to the predator overfishing interpretations of the Nova Scotian echinoid population fluctuations, *P. lividus* was the

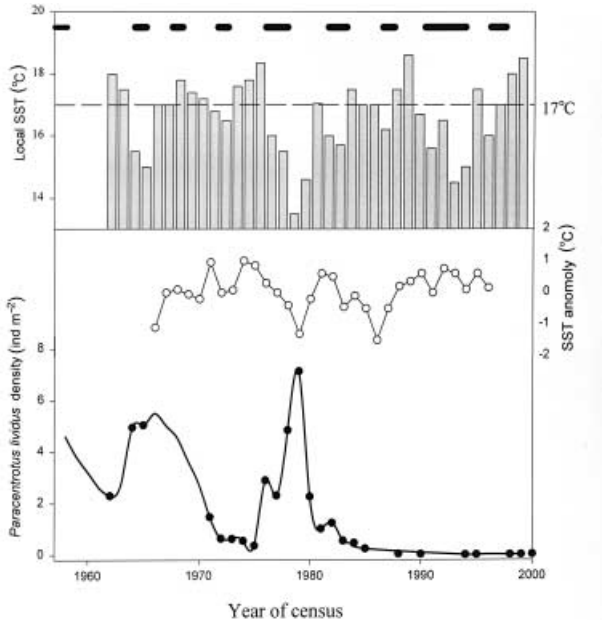

Figure 1 Population fluctuation of *Paracentrotus lividus* in the South Basin of Lough Hyne with sea temperature (°C) and ENSO events. *Paracentrotus lividus* census data from Muntz et al. (1965), Kitching (1987), Barnes et al. (1999) and 1999 point from present study. Lough Hyne sea surface temperature (local SST) data (grey bars) from Kitching (1987), Minchin (1992), Ballard & Myers (1997), unpublished sources and present study with threshold (17°C) for mass spawning in *P. lividus* superimposed (dashed line). Timing and duration of ENSO event data (black bars—top) from Glantz (1996); Irish Sea mean SST anomaly from Planque & Fox (1998).

actual target species (Southward & Southward, 1975; Byrne, 1990). Changes in oceanographic trends were later suggested to have been the major influence in the case of American east coast *Strongylocentrotus* population dynamics (Sheibling, 1986). Certainly the timing of population crashes of the Caribbean, Nova Scotian and Irish (Lough Hyne) echinoid populations coincided with major ENSO events. Along with other major echinoid populations, the Lough Hyne *P. lividus* population changed on a massive scale around the early 1980s. Furthermore, the other recorded Lough Hyne South Basin *P. lividus* population crash coincided with the influence of the 1965 (1969 and 1972) ENSO event (Figure 1). Neither the Irish nor the Caribbean and Nova Scotian populations have 'recovered' former levels of abundance since 1983. Periods of depressed maximum and mean SSTs typically accompany ENSO events on a local and regional scale. In contrast to Irish Sea cod (Planque & Fox, 1998), lowered SSTs reduce recruitment of *P. lividus* as a high critical temperature is needed for effective collective spawning. Whilst 'normal' years typically reach or exceed 17°C the sea temperatures are lower through the weakened Gulf Stream during ENSO events. Plankton tows from 1977 to 1981 by Minchin (1992) found many more echinoplutei larvae in the water column when the maximum annual sea temperature exceeded 17°C at Lough Hyne. Barnes et al. (1999) found significantly more 0+ cohort recruits in 1977 than during the prolonged ENSO influenced 1990s. Temperature fluctuations provide a mechanism for restriction of *P. lividus* populations by ENSO events and event timing is consistent with many of the population changes. Toxic dinoflagellate blooms are one suggested explanation for this. Whilst many 'red tides' appear to cause little negative influence on coastal organisms, others result in catastrophic mortality to benthos including to Irish *P. lividus* populations (Cross & Southgate, 1980).

The Lough Hyne *P. lividus* population represents one of the longest running databases of a specific urchin population and sea temperature. On balance we conclude that depressed SSTs may be causative of *P. lividus* population changes through spawning success and ultimately lack of recruitment. Large-scale cyclical oceanographic patterns, particularly those associated with ENSO events, should be considered as potentially important in long-term control of echinoid population levels, on a local and possibly a global-scale.

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