

## Using historical data to detect temporal changes in the abundances of intertidal species on Irish shores

Christina Simkanin<sup>\*†¶</sup>, AnneMarie Power<sup>‡</sup>, Alan Myers<sup>\*</sup>, David McGrath<sup>†</sup>, Alan Southward<sup>‡</sup>, Nova Mieszkowska<sup>‡</sup>, Rebecca Leaper<sup>§</sup> and Ruth O’Riordan<sup>\*</sup>

<sup>\*</sup>Department of Zoology, Ecology and Plant Science, National University of Ireland—Cork, Lee Maltings, Prospect Row, Cork City, Ireland. <sup>†</sup>Department of Life Sciences, Galway—Mayo Institute of Technology, Dublin Road, Galway, Ireland. <sup>‡</sup>Room 226, Martin Ryan Institute, National University of Ireland—Galway, Ireland. <sup>§</sup>Marine Biological Association of the United Kingdom, Citadel Hill, Plymouth, PL1 2BP, UK. <sup>¶</sup>Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia. <sup>¶</sup>Present address: Environmental Sciences and Resources, Portland State University, Portland, Oregon 97207-0751, USA. <sup>¶</sup>Corresponding author, e-mail: simkanin@pdx.edu

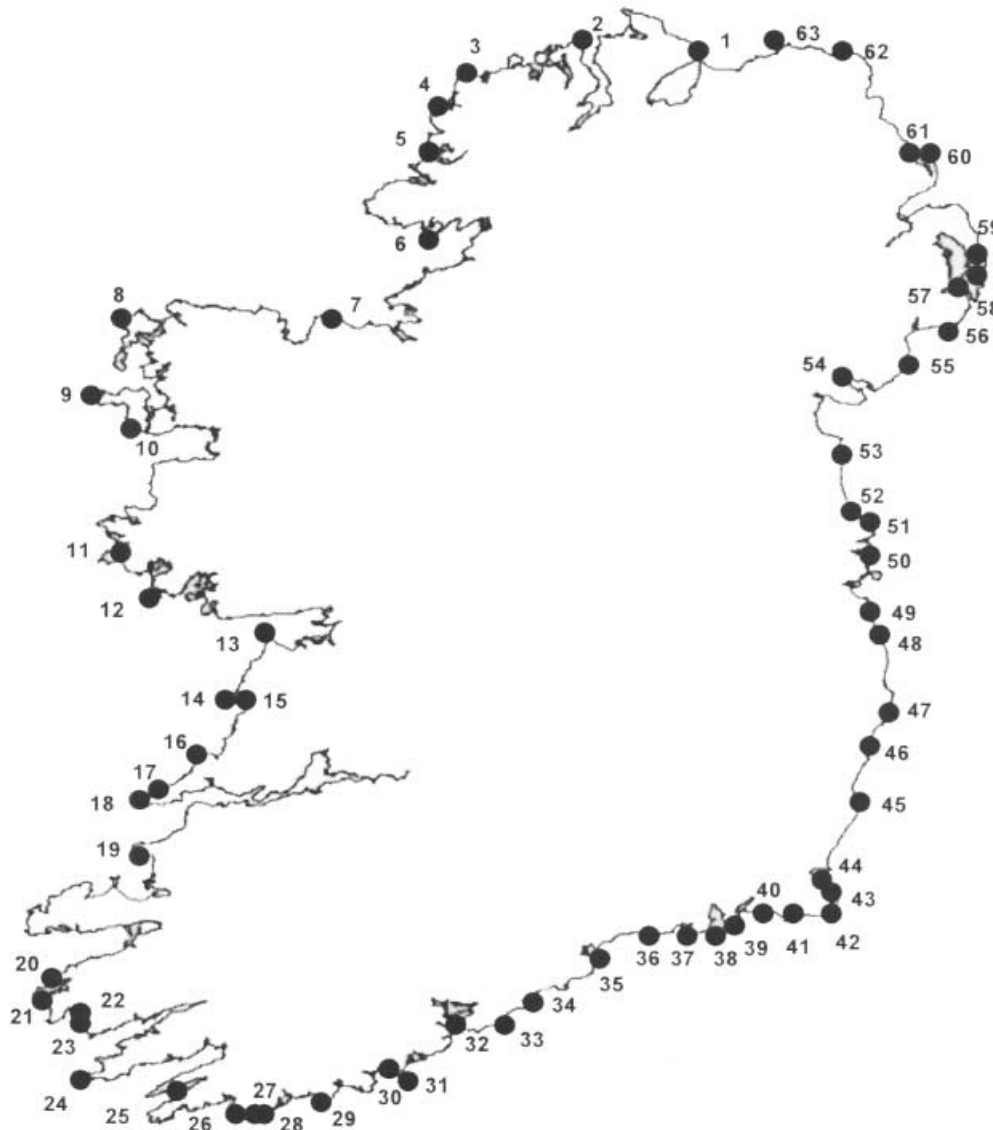
An historical data set, collected in 1958 by Southward and Crisp, was used as a baseline for detecting change in the abundances of species in the rocky intertidal of Ireland. In 2003, the abundances of each of 27 species was assessed using the same methodologies (ACFOR [which stands for the categories: abundant, common, frequent, occasional and rare] abundance scales) at 63 shores examined in the historical study. Comparison of the ACFOR data over a 45-year period, between the historical survey and re-survey, showed statistically significant changes in the abundances of 12 of the 27 species examined. Two species (one classed as northern and one introduced) increased significantly in abundance while ten species (five classed as northern, one classed as southern and four broadly distributed) decreased in abundance. The possible reasons for the changes in species abundances were assessed not only in the context of anthropogenic effects, such as climate change and commercial exploitation, but also of operator error. The error or differences recorded among operators (i.e. research scientists) when assessing species abundance using ACFOR categories was quantified on four shores. Significant change detected in three of the 12 species fell within the margin of operator error. This effect of operator may have also contributed to the results of no change in the other 15 species between the two census periods. It was not possible to determine the effect of operator on our results, which can increase the occurrence of a false positive (Type 1) or of a false negative (Type 2) outcome.

### INTRODUCTION

In recent years, studies demonstrating the possible effects of climate change on organisms have become more prevalent within the scientific literature (Parmesan & Yohe, 2003; Root et al., 2003). These data span terrestrial, freshwater and marine ecosystems and range from the tropics to the poles (Hughes, 2000; Wuethrich, 2000; Walther et al., 2002). Throughout the past century the average global surface temperature (the average of near surface land temperature and sea surface temperature) has increased by approximately 0.6°C and is predicted to continue increasing over the next 100 years by 1.2 to 3.5°C (Intergovernmental Panel on Climate Change [IPCC], 2001). Although the overall mean global temperature is increasing, it is believed that different regions will experience different climatic variations in relation to temperature and precipitation (Walther et al., 2002). Preliminary investigations of future climate scenarios for Ireland suggest that warming of approximately 0.2°C per decade, superimposed on an unknown ‘natural’ trend can be expected (Sweeney & Fealy, 2002). Knowledge of the direct effects of these rapid climate changes on biota is essential for future monitoring, conservation and for making reliable management decisions.

Due to Ireland’s location in the north-east Atlantic (52° to 55°N), it receives warm water from the North Atlantic Drift, resulting in mild air and sea temperatures compared with those of other countries at similar latitudes. The mild temperature allows both northern (cold-adapted) boreal species and southern (warm-adapted) Lusitanian species to coexist. Some of these northern and southern species reach the edge of their geographical distribution at or close to Ireland (Lewis, 1964). Species at the edge of their range are most likely to respond to fluctuations in physical factors such as climate, by changing in abundance (Fowler & Laffoley, 1993; Barry et al., 1995), or range (Lewis, 1986, 1996; Harrison et al., 2001b). Thus, Ireland can be considered an ideal location for studying change in rocky intertidal species abundances through time.

The intertidal is a good system for monitoring populations because it is well studied and thus the ecologies of intertidal species are well-known; the organisms are restricted to a narrow strip of shoreline habitat and therefore are easily tractable (Sagarin & Gaines, 2002); many of the species are mostly sessile or sedentary (Menge & Branch, 2001) and long-term monitoring is facilitated by their accessibility and visibility (Lewis, 1996). In addition, because it is the interface between land and sea, the intertidal experiences environmental pressures from both



**Figure 1.** Map of Ireland showing 63 shores surveyed during 1958 and 2003.

realms. As a consequence, fluctuations in temperature of both land and sea affect intertidal biota and predicting the effects of climate change on the intertidal may be even more difficult than it is on fully terrestrial or on fully marine species. Intertidal communities may be affected by sea level rise, increases in both seawater temperature and air temperature, increases in ultra-violet light penetration, and increases in storm activity, wave action and precipitation (Harrison et al., 2001a).

Essentially there are two types of data that are useful for investigating the long-term biological effects of climate change on biota: time series and baseline. Time series data (collected over a number of consecutive years) have been used to show the effect of climate change on a wide range of organisms, including plants (Bradley et al., 1999), insects (Parmesan et al., 1999), amphibians (Beebee, 1995; Visser et al., 1998), birds (Crick et al., 1997; Inouye et al., 2000), mammals (Post et al., 1997, 1999), fish (Genner et al., 2004) and marine zooplankton (Southward et al., 1995). However, collecting data over a series of years is

rare in ecological literature because it is time-consuming, costly and often not possible. Baseline data sets (once-off studies), on the other hand, are more prevalent in the literature because they require less effort to collect and are relatively inexpensive. Baseline studies have shown population responses to climate change, such as fluctuations in abundance and distribution limits (Parmesan, 1996; Sagarin et al., 1999).

This study utilized a historical baseline as a method for determining whether the abundances of intertidal organisms around the Irish coastline have been influenced by global climate warming. Empirical data are available suggesting that there has been a global warming trend throughout the last century (IPCC, 2001). If climate warming is affecting the intertidal biota of Ireland we would hypothesize that southern (warm-adapted) species would increase in abundance and extend their distributions beyond their current northern range limits, while northern (cold-adapted) species would experience declines in abundance and possible local extinctions at their southern range limits (Sagarin et al., 1999).

**Table 1.** Names and locations in latitude/longitude (dGPS) of the 63 Irish shores surveyed in both 1958 and 2003. Numbers correspond to Figure 1.

	Latitude	Longitude	Site name and county
1	55°17.65'N	007°07.708'W	Culdaff, Co. Donegal
2	55°16.678'N	007°38.197'W	Fanad Head, Co. Donegal
3	55°09.065'N	008°17.901'W	Bloody Foreland, north and south, Co. Donegal
4	55°02.168'N	008°23.077'W	Rinnalea Pt, Co. Donegal
5	54°55.942'N	008°26.823'W	Maghery-Termon, Co. Donegal
6	54°34.063'N	008°27.745'W	St Johns Pt, Co. Donegal
7	54°17.494'N	008°57.136'W	Easky, Co. Sligo
8	54°15.409'N	010°04.857'W	Termoncarragh, Co. Mayo
9	53°58.371'N	010°07.944'W	Dooagh Achill Island, Co. Mayo
10	53°52.556'N	009°57.991'W	Cloghmore Achill Sound, Co. Mayo
11	53°27.523'N	010°02.594'W	Mannin Bay, Co. Galway
12	53°24.228'N	010°06.999'W	Bunowen Pt, Co. Galway
13	53°09.264'N	009°15.847'W	Black Head, Co. Clare
14	52°55.898'N	009°28.415'W	Cangregga, Co. Clare
15	52°56.074'N	009°25.753'W	Furreera, Co. Clare
16	52°44.698'N	009°31.892'W	Doonbeg, Co. Clare
17	52°39.418'N	009°43.334'W	Castle Pt, Co. Clare
18	52°35.110'N	009°52.365'W	Moneen, Co. Clare
19	52°23.795'N	009°54.668'W	Kerry Head, Co. Kerry
20	51°56.680'N	010°16.610'W	Lough Kay, Doulus Bay, Co. Kerry
21	51°53.027'N	010°23.618'W	Portmagee Channel, opposite Bray Head, Co. Kerry
22	51°45.626'N	010°08.528'W	Abbey Island, Derrynane, Co. Kerry
23	51°46.259'N	010°01.253'W	Daniels Island, near Whitestrand, Co. Kerry
24	51°36.209'N	010°02.679'W	Whiteball Head Bay, Co. Cork
25	51°47.613'N	008°11.726'W	Gleen, Co. Cork
26	51°29.883'N	009°17.157'W	Tranabo Pier, Co. Cork
27	51°29.007'N	009°14.100'W	Toe Head, Co. Cork
28	51°29.055'N	009°14.479'W	Toe Head Bay, Co. Cork
29	51°31.774'N	008°57.266'W	Galley Head, Co. Cork
30	51°37.426'N	008°33.656'W	Ringalurisky Pt, Co. Cork
31	51°36.346'N	008°32.046'W	Old Head of Kinsale, Co. Cork
32	51°29.585'N	009°42.262'W	Gyleen, Co. Cork
33	51°49.605'N	008°00.049'W	Ballycotton, Co. Cork
34	51°53.105'N	007°51.976'W	Knockadoon Head, Co. Cork
35	52°03.284'N	007°32.439'W	Helvick Head, Co. Cork
36	52°08.315'N	007°22.245'W	Bunmahon, Co. Waterford
37	52°07.749'N	007°06.210'W	Brownstown Head, Co. Waterford
38	52°07.439'N	006°55.871'W	Hook Head, Co. Wexford
39	52°10.491'N	006°50.233'W	Baginbun Head, Co. Wexford
40	52°12.875'N	006°43.843'W	Cullenstown Reef, west, Co. Wexford
41	52°10.379'N	006°35.630'W	Forlorn Pt/Crossfarnoge, Co. Wexford
42	52°10.427'N	006°21.938'W	Carnsore Pt, Co. Wexford
43	52°14.439'N	006°18.821'W	Greenore Pt, Co. Wexford
44	52°14.722'N	006°19.487'W	Rosslare Harbour, Waddingsland Pt, Co. Wexford
45	52°34.111'N	006°11.993'W	Cahore Pt, Co. Wexford
46	52°44.229'N	006°08.607'W	Kilmichael Pt, Co. Wexford
47	52°55.744'N	006°01.328'W	Ardmore Pt, Co. Wicklow
48	53°08.900'N	006°03.712'W	Greystones, Co. Wicklow
49	53°11.791'N	006°05.300'W	Bray, Co. Wicklow
50	53°35.141'N	006°06.202'W	Skerries, Co. Dublin
51	53°27.100'N	006°08.472'W	Malahide Coast, Co. Dublin
52	53°36.974'N	006°10.991'W	Balbriggan, Co. Dublin
53	53°47.847'N	006°13.223'W	Port Oriel, Clougherhead, Co. Louth
54	54°05.901'N	006°12.600'W	Rosstrevor, Co. Down
55	54°06.264'N	005°53.784'W	Annalong, Co. Down
56	54°13.719'N	005°39.145'W	St Johns Pt, Co. Down
57	54°20.182'N	005°32.465'W	Kilclief, Co. Down
58	54°23.233'N	005°27.533'W	Kearney Pt, Co. Down
59	54°29.399'N	005°26.123'W	Townhead, across from Burial Island, Co. Down
60	54°50.904'N	005°43.678'W	Portmuck, Co. Antrim
61	54°52.134'N	005°48.801'W	Larne, Glenarm A2 coastal Rd, Co. Antrim
62	55°12.652'N	006°11.670'W	Marconi's Cottage, Co. Antrim
63	55°12.746'N	006°39.475'W	Portrush, Co. Antrim

**Table 2.** *Abundance categories derived by Crisp & Southward (1958) and used throughout the 1958 and 2003 surveys.*

Species	Abundance category				
	Abundant	Common	Frequent	Occasional	Rare
<b>Barnacles</b>					
<i>Chthamalus stellatus</i> , <i>Chthamalus montagui</i> , <i>Semibalanus balanoides</i> , <i>Elminius modestus</i>	> 1 per cm <sup>2</sup> ; rocks well covered	0.1–1.0 per cm <sup>2</sup> ; up to 1/3 of rock space covered	0.01–0.1 per m <sup>2</sup> individuals never more than 10 cm apart	0.0001–0.01 per cm <sup>2</sup> ; few within 10 cm of each other	Less than 1 per m <sup>2</sup> only a few found in 30 min search
<b>Limpets</b>					
<i>Patella vulgata</i> , <i>Patella ulyssiponensis</i>	Over 50 per m <sup>2</sup> or more than 50% of limpets at certain levels	10–50 per m <sup>2</sup> , 10% to 50% at certain levels	1–10 per m <sup>2</sup> , 1% to 10% at certain levels	Less than 1 per m <sup>2</sup> on average, less than 1% of population	Only a few found in 30 min search
<b>Topshells</b>					
<i>Osilinus lineatus</i> , <i>Gibbula umbilicalis</i> , <i>Gibbula cineraria</i>	Exceeding 10 per m <sup>2</sup> generally	1–10 per m <sup>2</sup> , sometimes very locally over 10 per m <sup>2</sup>	Less than 1 per m <sup>2</sup> , locally sometimes more	Always less than 1 per m <sup>2</sup>	Only a few found in 30 min search
<b>Periwinkles</b>					
<i>Littorina littorea</i>	More than 50 per m <sup>2</sup>	10–50 per m <sup>2</sup>	1–10 per m <sup>2</sup>		Only a few found in 30 min search
<b>Anenomes</b>					
<i>Anemonia viridis</i>	Many in almost every pool and damp place	Groups in pools and damp places	Isolated specimens in few pools		A small number under 10, found after 30 min search
<b>Algae and <i>Mytilus</i> spp.</b>	> 30%	5–30%	< 5%	Scattered individuals	Few plants 30 min search

We used a previously unpublished intertidal dataset, collected by Southward & Crisp in 1958, as a baseline to detect change in the geographical distribution of selected biota. Southward & Crisp devised and utilized a sampling protocol for assessing intertidal species semi-quantitatively according to categories of abundance (Crisp & Southward, 1958). This method is commonly called ACFOR, which stands for the categories: abundant, common, frequent, occasional and rare. A sixth category 'not seen' was also employed. The ACFOR methodology is applicable to both flora and fauna on rocky shores, however, it is often restricted to conspicuous species. A major advantage of using the ACFOR method, is that the number of shores that can be assessed in a given time over an extensive geographical area is increased, compared with fully quantitative methods. The method, because of its generality, is also readily useable on rocky shores of varying physical attributes (e.g. topographical heterogeneity and wave exposure). In addition, because there are only six categories, each with its own quantitative description, different operators should be able to attribute categories accurately. However, because each species is assessed in a subjectively chosen area of shore, the 'zone of most abundance' (Southward & Crisp, 1954) results can vary among operators (Baker et al., 1981; Foster-Smith & Evans, 2003). This potential variation among operators will be most important when shores are re-surveyed, perhaps several times, over a long time period, and where different volunteers or operators are used to quantify species abundances at each census. Another potential operator bias may stem from the interpretation of each abundance category

(Foster-Smith & Evans, 2003). This can become especially critical when species are near the limits (upper or lower) of a category. Workers must make a decision on which category to place the species counts in, perhaps one higher or one lower than another operator. A consequence of the ACFOR method is that there is no measure of within-shore variability, thus each shore becomes a replicate within a large spatial scale. Therefore, the robustness of the method increases when there are many shores surveyed over large (greater than regional) spatial scales.

The aims of the 2003 re-survey were: (1) to investigate changes in the abundance of intertidal organisms around the Irish coast after a 45-year time interval; (2) to assess whether any of these changes were consistent with expected anthropogenic effects, such as global climate warming; and (3) to determine how much error in recorded abundance data could be attributed to operator differences.

## MATERIALS AND METHODS

### *Study area and species*

During the historical survey (conducted in 1958), 150 shores were surveyed around the Irish coastline and the abundance of a total of 53 intertidal invertebrate and algal species was assessed. However, on many of the shores in 1958, only a subset of the 53 species were counted. In the 2003 re-survey, therefore, only 27 species that had been recorded on a regular basis, were counted. As each of the selected 27 species was not sampled on

**Table 3.** The frequency of abundance scores for each of the 27 species re-surveyed during 2003. Although the re-survey estimated the abundance of all 27 species at 63 sites, only those sites where the species was recorded in 1958 were used during calculations. *Chthamalus montagui* and *Chthamalus stellatus* are combined as *Chthamalus spp.*

	1958						2003						Total	Change in abundance
	A	C	F	O	R	NS	A	C	F	O	R	NS		
Northerly species														
<i>Alaria esculenta</i>	16	7	2	4	1	16	10	1	1	5	4	25	46	Decrease***
<i>Ascophyllum nodosum</i>	5	8	1	4	1	1	8	5	1	0	0	6	20	
<i>Balanus crenatus</i>	2	8	0	3	0	3	0	0	0	0	0	16	16	Decrease****
<i>Chondrus crispus</i>	8	9	0	2	2	1	9	5	3	1	3	1	22	
<i>Halidrys siliquosa</i>	20	9	0	4	0	10	18	0	2	5	5	13	43	
<i>Himanthalia elongata</i>	19	11	3	5	0	15	24	1	0	2	0	26	53	
<i>Laminaria hyperborea</i>	7	5	1	2	0	0		1	0	1	1	11	15	Decrease***
<i>Laminaria saccharina</i>	10	11	3	4	0	0	2	6	1	6	2	11	28	Decrease****
<i>Littorina littorea</i>	27	8	1	0	0	1	15	12	7	0	1	2	37	Decrease***
<i>Mastocarpus stellatus</i>	11	13	0	2	1	0	16	0	3	4	1	3	27	
<i>Nucella lapillus</i>	27	11	1	2	0	1	27	7	4	2	2	0	42	
<i>Semibalanus balanoides</i>	30	15	4	2	1	5	42	8	2	1	2	2	57	Increase*
Southerly taxa														
<i>Anemonia viridis</i>	8	3	3	5	5	32	11	5	4	1	9	26	56	
<i>Bifurcaria bifurcata</i>	5	1	2	1	1	28	7	0	0	0	0	31	38	
<i>Chthamalus spp.</i>	44	11	3	2	1	1	48	5	4	0	2	3	62	
<i>Cystoseira spp.</i>	4	3	0	3	0	24	3	1	0	2	0	28	34	
<i>Gibbula umbilicalis</i>	28	10	2	4	3	8	28	10	6	0	6	5	55	
<i>Osilinus lineatus</i>	18	6	3	5	1	17	15	6	2	2	9	16	50	
<i>Paracentrotus lividus</i>	16	1	2	0	1	35	5	3	6	1	2	38	55	Decrease**
<i>Patella ulyssiponensis</i>	23	6	3	6	1	0	15	9	10	2	1	2	39	
<i>Sabellaria alveolata</i>	4	3	2	4	0	15	5	1	0	1	0	21	28	
Broadly distributed taxa														
<i>Calliostoma zizyphinum</i>	1	0	0	7	0	6	0	0	0	0	6	9	15	Decrease*
<i>Codium spp.</i>	9	2	2	1	0	0	2	1	1	1	0	7	12	Decrease***
<i>Gibbula cineraria</i>	13	19	1	3	0	5	4	8	6	9	7	7	41	Decrease****
<i>Melarhaphé neritoides</i>	29	10	10	4	0	3	30	4	1	0	1	12	48	Decrease**
<i>Mytilus spp.</i>	28	4	4	10	0	5	31	3	3	7	3	2	49	
Introduced species														
<i>Elminius modestus</i>	0	0	0	2	3	33	1	4	5	6	7	15	38	Increase****

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.005$ ; \*\*\*\*,  $P < 0.001$ .

every shore during the 1958 survey only those shores with at least 15 species recorded were chosen. This resulted in 63 shores being re-surveyed (Figure 1 and Table 1).

Fieldwork was carried out from March to November 2003 around the entire Irish coastline. One team consisting of two operators conducted the re-survey. A second team, also consisting of two operators, sampled a subset of four shores in order to allocate team operator error (see below). All four persons were highly experienced intertidal scientists. A 'standard sampling protocol' was used which was developed in conjunction with one of the original recorders (A.J.S.). In order to ensure that the methodology used by each team was comparable, two separate 'training' days were completed. During these days the sampling protocol and identification of species were rigorously standardized.

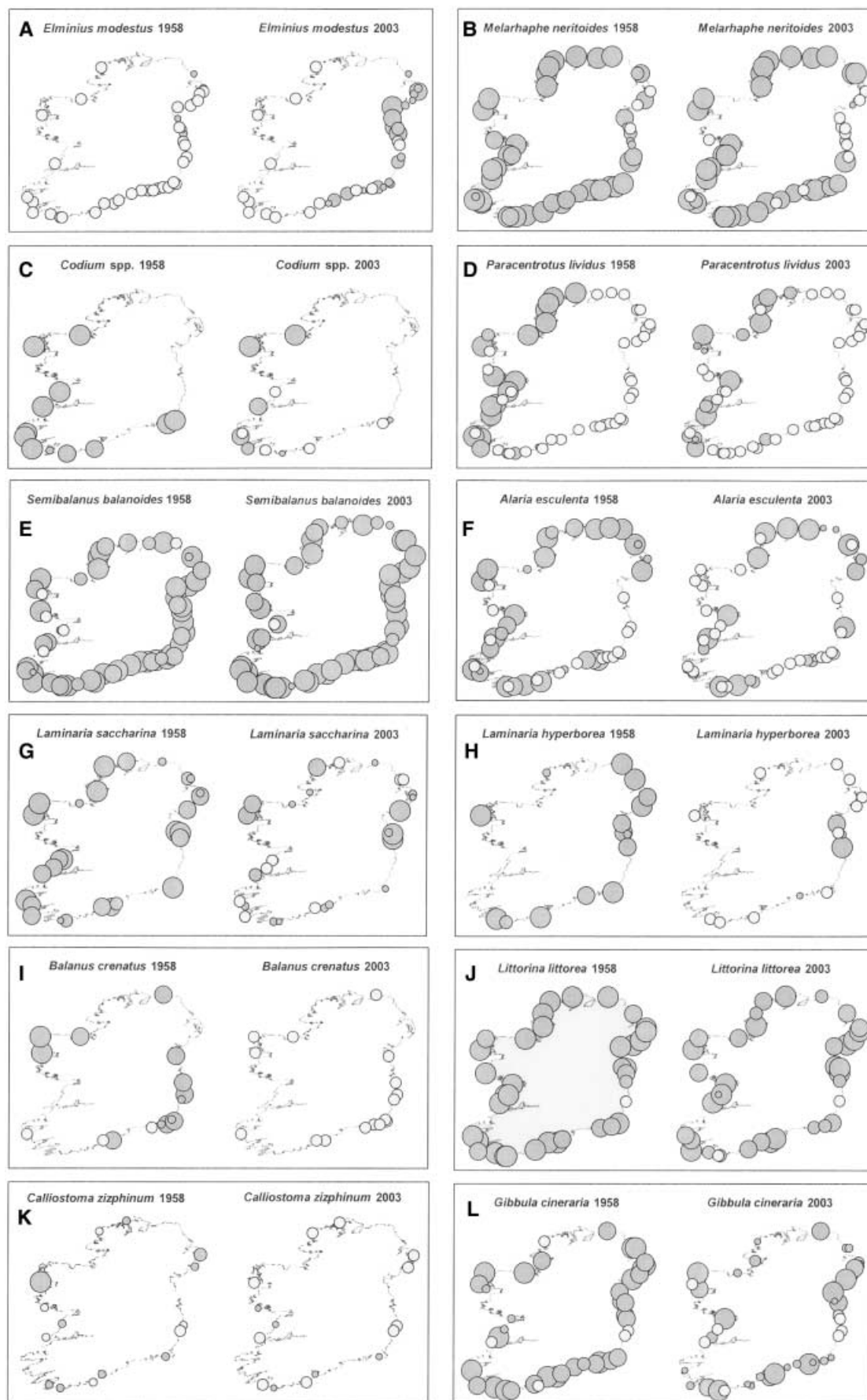
#### Data collection

Shores were sampled at low water during spring tides to allow for an adequate estimate of lower shore species abundances. Each shore was located using the data documented during 1958, including the latitude and longitude

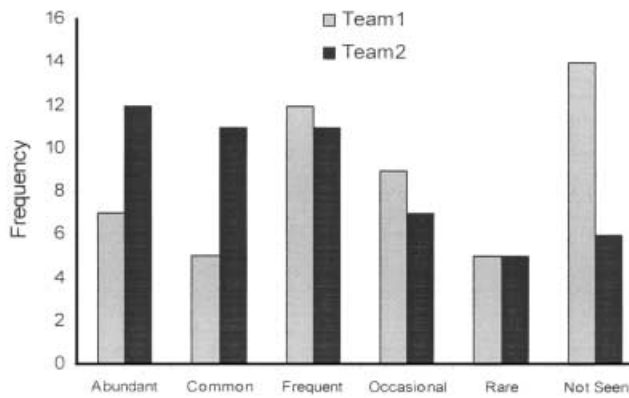
of each shore, and shore and species descriptions. Once relocated, two Global Positioning System (GPS) readings were taken for each shore, one at the access point (dGPS) and another at the centre of the shore being sampled. Digital photographs were taken to show the approach and the general view of each shore. At each shore, 27 intertidal species (or genera in the case of species which could not be identified to species level i.e. *Cystoseira* spp., *Mytilus* spp.) were quantified. The abundance scales used were those devised by Southward & Crisp during the early 1950s and published in 1958 (Crisp & Southward, 1958; Table 2). Each species was assigned to an ACFOR category within its 'zone of most abundance'. On average, both operators spent an hour searching and recording abundances on each shore. Species were given an abundance score after two hours of sampling effort and if a species was not found during that time it was recorded as not seen.

#### Data analysis

During data collection, *Chthamalus stellatus* (Poli) and *Chthamalus montagui* Southward were identified and



**Figure 2.** (A–L) The distribution and abundance (using the ACFOR scale) of 12 species that showed a significant change in abundance between 1958 and 2003 (based only on shores that were sampled during both surveys). ○, Not seen, ◊, Rare; ◐, Occasional; ◑, Frequent; ◒, Common; ◓, Abundant.



**Figure 3.** Operator error differences in the frequency of abundance categories allocated between two teams, of two individuals each, within the same area on consecutive days at four shores.

assessed separately. They were, however, combined as *Chthamalus* spp. throughout the analysis, because the two species were not separated at the time of the initial baseline survey. Species were grouped as northern, southern or broadly-distributed to reflect their geographical range distribution. Northern species were defined as those whose geographical range extended from the Arctic Circle south to northern Portugal. Southern species

extended from North Africa north as far as Scotland. Broadly distributed species had ranges extending from Norway to North Africa or the Mediterranean (Hayward et al., 1996; Gibson et al., 2001).

The abundance scale (ACFOR) produces categorical data which are best analysed using non-parametric statistical tests. The paired Wilcoxon signed-ranks test was used to test for changes in the abundance of each of the 27 species between 1958 and 2003 (see Pearson et al., 1985 for similar approach). Only shores where a species was recorded during both time periods (including shores where it was found to be ‘not seen’) were used during analysis. This was because a search for every species on each shore during the 1958 survey was not done, resulting in differences in the number of observations for each species. Data for the Wilcoxon signed-ranks test, involved assigning numbers to the ACFOR categories as follows: abundant=5, common=4, frequent=3, occasional=2, rare=1 and not seen=0.

*Operator error*

A sub-sample of four shores in Northern Ireland was used to determine the amount of potential variability in ACFOR scores attributable to between-team operator differences. An estimation of error between teams, each made-up of two trained individuals, involved each team

**Table 4.** Number and percentage differences in allocating an ACFOR category. Shores were sampled by teams (of two trained individuals) sampling the same area on consecutive days. The standard deviation is also shown.

Shore	Number of species assessed per shore	Number assessed differently	Percentage difference	Differences of > 1 category	Per cent difference of > 1 category
1	54	8	14.81	5	9.26
2	53	12	22.64	9	16.98
3	54	15	27.78	12	22.22
4	54	17	31.48	10	18.52
Mean	53.75 ±50.5	13 ±3.9	24.18 ±7.2	9 ±2.9	16.75 ±5.5

**Table 5.** Listed are the 12 species that showed a significant change in abundance from 1958 to 2003. Shown are the number and percentage of times an ACFOR category differed from 1958 to 2003 as well as the number and percentage of times an ACFOR category differed by greater than one category. The three species in bold are those that fall within the percentage of operator error (22.22%) when allocating ACFOR categories of more than one magnitude of difference.

Species name	Number of shores recorded	Number of differences from 1958 to 2003	Percentage difference	Differences of > 1 category	Per cent difference of > 1 category
<i>Alaria esculenta</i>	15	12	80.00	12	80.00
<i>Balanus crenatus</i>	12	10	83.33	8	66.67
<i>Calliostoma zizyphinum</i>	28	26	92.86	17	60.71
<i>Codium</i> spp.	47	25	53.19	21	44.68
<b><i>Elminius modestus</i></b>	57	30	52.63	12	<b>21.05</b>
<i>Gibbula cineraria</i>	16	13	81.25	10	62.50
<i>Laminaria hyperborea</i>	38	21	55.26	15	39.47
<i>Laminaria saccharina</i>	41	33	80.49	21	51.22
<i>Littorina littorea</i>	15	10	66.67	5	33.33
<b><i>Melarhaphé neritoides</i></b>	48	20	41.67	7	<b>14.58</b>
<i>Paracentrotus lividus</i>	37	22	59.46	16	43.24
<b><i>Semibalanus balanoides</i></b>	55	17	30.91	4	<b>7.27</b>

surveying the same shores on consecutive days. Each team was required to locate shores independently using the information provided from the 1958 survey. The difference recorded on these shores was then used to calibrate for differences between the 1958 and 2003 surveys.

The percentage error when allocating abundance categories was quantified between teams of operators. Specifically the differences of more than one category (i.e. more than one order of magnitude) were assessed. When using abundance scales differences of more than one category are presumed to be significant (Baker et al., 1981). The operator error percentage was then used to estimate the amount of difference expected when any two teams allocated abundance categories. If any species showed an apparently significant change after 45 years the data were analysed to determine if operator error could have affected the results. This was carried out by determining the number and percentage of times an ACFOR category differed from 1958 to 2003 for each species. To assess the effect of operator error, the percentage of differences measured between teams of operators was compared with the percentage of differences in abundance categories for each species.

## RESULTS

### *Species' changes after 45 years*

Overall, 12 of the 27 species showed a significant change in their abundance (Table 3). According to the distribution classification, five northern species *Alaria esculenta* (L.), *Balanus crenatus* Bruguière, *Laminaria hyperborea* (Gunnerus) Foslie, *Laminaria saccharina* (L.) Lamouroux, *Littorina littorea* (L.), one southern species *Paracentrotus lividus* (Lamarck), and four broadly-distributed species *Calliostoma zizyphinum* (L.), *Gibbula cineraria* (L.), *Codium* spp., *Melarhaphé neritoides* (L.) showed a significant decrease in abundance from 1958 to 2003. In contrast, one northern species *Semibalanus balanoides* (L.) and one introduced species, *Elminius modestus* Darwin, showed an increase in abundance. Overall, 15 species showed no significant change in abundance from 1958 to 2003. Six were northern species (*Ascophyllum nodosum* (L.) Le Jolis, *Chondrus crispus* Stackhouse, *Halidrys siliquosa* (L.) Lyngbye, *Himantalia elongata* (L.) Gray, *Mastocarpus stellatus* (Stackhouse) Guiry and *Nucella lapillus* (L.)), eight were southern taxa (*Anemonia viridis* (Forsskål), *Bifurcaria bifurcata* Ross, *Chthamalus* spp., *Cystoseira* spp., *Gibbula umbilicalis* (da Costa), *Osilinus lineatus* (da Costa), *Patella ulyssiponensis* Gmelin, *Sabellaria alveolata* (L.)) and one (*Mytilus* spp.) was a broadly distributed taxon.

Spatial changes in species abundances are shown in Figure 2A–L. Four of the species showed a clear geographical trend in change. The introduced barnacle species *E. modestus* (Figure 2A) increased everywhere, especially along the east coast. The broadly distributed *Codium* spp. decreased along the south and south-western coastline (Figure 2B). *Melarhaphé neritoides*, also a broadly distributed species, decreased predominantly along the east coast (Figure 2C). *Paracentrotus lividus*, a southern species, decreased along the west coast (Figure 2D) and the other seven species showed changes but in no consistent geographical pattern. The northern species *Semibalanus balanoides*

(Figure 2E) showed an overall increase while the other northern species *Alaria esculenta* (Figure 2F), *Laminaria saccharina* (Figure 2G), *L. hyperborea* (Figure 2H), *Balanus crenatus* (Figure 2I) and *Littorina littorea* (Figure 2J) showed decreases over the entire coastline. The two broadly distributed species *Calliostoma zizyphinum* (Figure 2K) and *G. cineraria* (Figure 2L) also showed decreases over the entire coastline.

### *Operator error*

While using the ACFOR categories to assess species abundances, teams tended to differ most often when allocating the abundant, common and not seen categories, whereas they were more consistent when assigning the frequent, occasional and rare categories (Figure 3). Two teams working on the same shore attributed a different abundance category 24.18% of the time (Table 4) and 16.75% of the total differences involved changes of more than one category.

It was important to determine whether the 12 species, which showed a significant change in abundance from 1958 to 2003, were affected by operator error. Each of the 12 species was assessed for the number of times an abundance score was attributed differently by one or more categories from 1958 to 2003 (Table 5). The percentage change observed in three species: *E. modestus*, *M. neritoides* and *S. balanoides*, was actually less than the percentage difference between teams of operators. Thus the significant change in abundance shown by the analysis for these three species may be due to sampling error. The other eight species did not fall within the range of error due to sampling by different teams, however, the significance level of the change shown by these species may have been increased or decreased due to the effects of sampling error. As well, it is possible that the 15 species which showed no significant change during analysis were also affected by operator differences, leading to a falsely negative (non-significant) result. However, it is not possible to determine the extent to which operator differences affected these results.

## DISCUSSION

### *Species' changes after 45 years*

Five species conformed to our hypothesis that if global climate warming was having an effect on intertidal biota southern species would increase in abundance and range while northern species would decrease in abundance and range. These five species were northern species: the algae *Alaria esculenta*, *Laminaria saccharina* and *Laminaria hyperborea*, the barnacle *Balanus crenatus*, and the gastropod *Littorina littorea*. All five species showed decreases over the entire coastline suggesting that the cause of their decrease might be linked to processes that act over a large scale. The growth and survival of both *A. esculenta* and *Laminaria saccharina* have been shown to be negatively affected by ultraviolet (UV) radiation, especially in shallow water or low-tidal conditions (Makarov, 1999; Michler et al., 2002; Apprill & Lesser, 2003). Although not a direct effect of a warming climate, the regeneration of the ozone layer is inhibited by greenhouse gases which



drive climate change (Shindell et al., 1998; Clarke & Harris, 2003). As the ozone layer continues to decrease, the levels of UV radiation reaching the earth's surface are set to increase (Clarke & Harris, 2003). Increases in UV radiation affect many aquatic species including phytoplankton (Häder et al., 1998), corals (Brown et al., 1994), amphibians (Blaustein et al., 2000), sea urchins (Adams, 2001; Verling et al., 2002) and anemones (Westholt et al., 1999). The species, *A. esculenta*, *L. saccharina*, *L. hyperborea* and *B. crenatus* are all shallow sublittoral inhabitants and are generally only easily seen during extreme low tides. It is possible, therefore, that the abundance of these species may have been underestimated. However, this underestimation would have also occurred during the 1958 survey and therefore should not have affected the results. The northern gastropod *Littorina littorea* decreased significantly around the whole of the Irish coastline, most likely as a direct result of its commercial exploitation. This species is collected on virtually all Irish coasts for export to mainland Europe (Fisheries Science Services, 2003). The biomass of *L. littorea* collected commercially has fluctuated since the 1970s but overall, there has been a decline in exploitation with 2400 tonnes being collected in 1970 and only 1368 tonnes being collected in 2003 (Fisheries Science Services, 2003).

The only southern species to decrease significantly was the sea urchin *Paracentrotus lividus*. This sea urchin is only found along the western and southern Irish coastline where it has decreased from 1958 to 2003. *Paracentrotus lividus* is another commercially important species and in 1976, 375 tonnes were landed in Ireland (Fisheries Science Services, 2003). Since then a rapid decline in the abundance of *P. lividus* has occurred and during 2000 only 0.7 tonnes were landed (Fisheries Science Services, 2003). This decline is believed to be due to a combination of the over-exploitation and the slow growth rate of the species (Southward & Southward, 1975). However, there is an indication that *P. lividus* populations are being affected by factors other than over-exploitation. A recent study at Lough Hyne Marine Nature Reserve, where the removal of any organism within the reserve boundaries is prohibited, showed a decrease in *P. lividus* from the 1970s to present (Barnes et al., 2002). The reasons for this decrease may be related to sea surface temperatures and population fragmentation (Barnes et al., 2002).

The broadly distributed species, *Calliostoma zizyphinum*, *Gibbula cineraria*, *Melarhaphé neritoides* and *Codium* spp. also declined in abundance. In particular, the trochids *Calliostoma zizyphinum* and *G. cineraria* both showed decreases in abundance over the entire coastline suggesting that they are being affected by large-scale processes. Both trochid species may be responding to a decrease in the algae (*A. esculenta*, *Laminaria saccharina* and *L. hyperborea*), which may be used as a food or shelter resource. Again, *C. zizyphinum* and *G. cineraria* are lower shore and shallow sublittoral species, and it is possible that the recorded decrease in abundance is a sampling artefact. In addition, both species can be rare in the intertidal making them difficult to assess. The littorinid *M. neritoides* also decreased throughout the coastline and was not found along the east coast at the sites surveyed. The decrease in *M. neritoides* fell within the range of operator error, therefore the apparent decrease may be an

artefact. There are three taxa of *Codium* in Ireland, two are introduced (*Codium fragile* ssp. *tomentosoides* and *Codium fragile* ssp. *atlanticum*) and one is native, with a southern distribution (*Codium tomentosum*) (Trowbridge, 2001). Distinguishing between the three taxa in the field is difficult. It generally requires a specimen to be brought back to the laboratory for identification. In this survey, all *Codium* species in the field were recorded as *Codium* spp. Both introduced species were present in Ireland before the 1958 survey (Silva, 1955; Trowbridge, 2001), but, due to the same difficulties with identification, all findings were recorded then as *Codium* spp. The comparison between 1958 and 2003 has shown a decrease in *Codium* spp. along the south-east and south-west coastline. The fact that there are three taxa in Ireland makes it difficult to interpret this decrease in abundance.

Two barnacle species, one introduced and one native, showed an increase in abundance between 1958 and 2003. The increase of *Elminius modestus* around the Irish coastline has been well documented since it was introduced with shipping in 1955 (Crisp, 1958; O'Riordan, 1996). *Elminius modestus* is known to have a number of competitive advantages over native barnacle species including a year round breeding season and a tolerance to varied salinities (Lawson et al., 2004). Therefore, the significant increase of *E. modestus* may be a classic example of a successful invasion, reflecting a rapid colonization of a new area by a non-native species entirely unrelated to climate change. However, studies have shown that climate change may indirectly affect the interactions between introduced and native species by causing increased stress in native populations (Occhipinti-Ambrogi & Savini, 2003) and earlier recruitment in introduced species (Stachowicz et al., 2002). The barnacle *Semibalanus balanoides*, is a northern species native to western Europe and therefore might have been expected to decrease in abundance given increases in average global surface temperatures (IPCC, 2001). A direct link between fluctuating temperature regimes and the abundance of *S. balanoides* has been shown by Southward (1991), whereby *S. balanoides* flourishes during cold temperature periods, while during warm temperature periods it decreases in abundance. Globally the 1990s was the warmest decade and 1998 was the warmest year since 1861 (IPCC, 2001), suggesting that *S. balanoides* should have decreased in abundance in response to the warming trends. The detected increase in abundance may be a consequence of the abundance scale methodology used. Operator error analysis suggests that methodological issues may have played a role in the apparent increase in both *E. modestus* and *S. balanoides* (see below).

It was not possible to draw robust conclusions about species fluctuations and anthropogenic effects because of the existence of only two data points spanning 45 years. Long-term trends in species abundances are often obscured by short-term fluctuations (Lesica & Steele, 1996) and for this reason, it is difficult to interpret the observed changes.

#### Operator error

There is good consistency between teams of operators in attributing the categories 'frequent', 'occasional' and 'rare',

whereas there is a greater inconsistency when attributing the categories 'abundant', 'common' and 'not seen'. The high discrepancy between teams of operators when allocating the 'not seen' category has implications for identifying species apparent limits of distribution. It is clear that 'rare' and 'occasional' species may be missed, especially at their range edges where species tend to be low in abundance. They may, therefore, be recorded as 'not seen' when in fact they are present. Because there is no quantified sampling area within and between shores or sampling time for each species listed for survey, it is possible that operators are sampling different area extents when on the shore. If the shore and sampling area were clearly determined before conducting the survey, it would greatly decrease the probability of methodological error. Another potential problem concerns defining the 'zone of most abundance', which, could be considered a different size by each operator.

The error recorded between teams of two individuals was considerable. Teams had to locate shores individually using the data supplied from the historical survey, while undertaking sampling on consecutive days so that the actions of one team were completely independent of the other. Therefore, it is possible that teams were sampling different areas of shores. This possibility also exists between the 1958 baseline survey and the 2003 re-survey. By applying modern techniques, such as GPS and digital photography, relocation of shores on any future survey will be more accurate and therefore may reduce the amount of sampling error encountered.

Our results indicated that the significant difference in the abundance of three species (*E. modestus*, *S. balanoides* and *M. neritoides*) may have been caused by operator error and not a change due to natural or anthropogenic reasons. The effect of operator error may be decreased if the significance levels for examining change were increased from 95% to 99%. However, this does not affect conclusions reached for *E. modestus*, which showed a very significant change.

#### *Summary and conclusions*

The recorded abundance of 12 intertidal species has changed after a 45-year time interval. Processes responsible for the changes have been postulated and include climate warming, commercial exploitation and sampling error. For three species, the error attributed to sampling effort was much greater than that attributed to change in abundance alone. The subjective definition of 'zone of most abundance', may contribute to sampling error.

No single ecological study has demonstrated that climate change is irrefutably causing the recent biological changes to species and communities (Hughes, 2000; McCarty, 2001), although there is mounting evidence to support climate-induced impacts on species populations (Parmesan, 1996). Although ecologists recognize that long-term datasets may allow for more unequivocal impact studies, these are relatively sparse (Hughes, 2000). The study presented here has demonstrated not only the value of revisiting an historical baseline survey to assess change in species abundances in different decades, but has also provided a critical analysis of the existing sampling methodology, while creating a new and full

dataset which can be used as a baseline for future monitoring.

This study was carried out as part of the Marine Biodiversity and Climate Change (MarClim) project with the support of a post-doctoral fellow award to A.M.P. (PDOC/01/006) from October 2002–2005 from the Irish Marine Institute and the Marine RTDI Measure, Productive Sector Operational Programme, National Development Plan 2000–2006. We would like to thank Dr Tasman Crowe, Dr Elizabeth Gosling, Professor Steve Hawkins, Dr Ian Davidson and Dr Clare Lehané for helpful comments and/or field assistance.

#### REFERENCES

- Adams, N.L., 2001. UV radiation evokes negative phototaxis and covering behaviour in the sea urchin *Strongylocentrotus droebachiensis*. *Marine Ecology Progress Series*, **213**, 87–95.
- Apprill, A.M. & Lesser, M.P., 2003. Effects of ultraviolet radiation on *Laminaria saccharina* in relation to depth and tidal height in the Gulf of Maine. *Marine Ecology Progress Series*, **256**, 75–85.
- Baker, J.M. et al., 1981. The rocky shore biology of Bantry Bay: a resurvey. *Irish Fisheries Investigations Series B*, **23**, 3–27.
- Barnes, D.K.A., Verling, E., Crook, A., Davidson, I. & O'Mahoney, M., 2002. Local population extinction follows (20 years after) cycle collapse in a keystone species. *Marine Ecology Progress Series*, **226**, 311–313.
- Barry, J.P., Baxter, C.H., Sagarin, R.D. & Gilman, S.E., 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. *Science, New York*, **267**, 672–675.
- Beebe, T.J.C., 1995. Amphibian breeding and climate. *Nature, London*, **374**, 219–220.
- Blaustein, A.R., Chivers, D.P., Kats, L.B. & Kiesecker, J.M., 2000. Effects of ultraviolet radiation on locomotion and orientation in roughskin newts (*Taricha granulosa*). *Ethology*, **106**, 227–234.
- Bradley, N.L., Leopold, A.C., Ross, J. & Huffaker, W., 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 9701–9704.
- Brown, B.E., Dunne, R.P., Scoffin, T.P. & Le Tisser, M.D.A., 1994. Solar damage in intertidal corals. *Marine Ecology Progress Series*, **105**, 219–230.
- Clarke, A. & Harris, C.M., 2003. Polar marine ecosystems: major threats and future change. *Environmental Conservation*, **30**, 1–25.
- Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L., 1997. UK birds are laying eggs earlier. *Nature, London*, **388**, 526.
- Crisp, D.J., 1958. The spread of *Elminius modestus* Darwin in north-west Europe. *Journal of the Marine Biological Association of the United Kingdom*, **37**, 483–520.
- Crisp, D.J. & Southward, A.J., 1958. The distribution of intertidal organisms along the coasts of the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **37**, 157–208.
- Fisheries Science Services, 2003. *The stock book: annual review of fish stocks in 2003 with management advice for 2004*. Dublin, Ireland: Marine Institute.
- Foster-Smith, J. & Evans, S.M., 2003. The value of marine ecological data collected by volunteers. *Biological Conservation*, **113**, 199–213.
- Fowler, S. & Laffoley, D., 1993. Stability in Mediterranean–Atlantic sessile epifaunal communities at the northern limits of their range. *Journal of Experimental Marine Biology and Ecology*, **172**, 109–127.

- Genner, M.J., Sims, D.W., Wearmouth, V.J., Southall, E.J., Southward, A.J., Henderson, P.A. & Hawkins, S.J., 2004. Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society B*, **271**, 655–661.
- Gibson, R., Hextall, B. & Rogers, A., 2001. *Photographic guide to the sea and shore life of Britain and north-west Europe*. Oxford: Oxford University Press.
- Häder, D.-P., Kumar, H.D., Smith, R.C. & Worrest, R.C., 1998. Effects on aquatic ecosystems. *Journal of Photochemistry and Photobiology B*, **46**, 53–68.
- Harrison, P.A., Berry, P.A. & Dawson, T.P., ed., 2001a. *Climate change and nature conservation in Britain and Ireland: modelling natural resource responses to climate change (the MONARCH project)*. Oxford: UKCIP Technical Report.
- Harrison, P.A., Berry, P.M., Viles, H.A., Austin, G.E., Hossell, J.E. & Rehfish, M.M., 2001b. Overview of impacts, adaptation and vulnerability. In *Climate change and nature conservation in Britain and Ireland: modelling natural resource responses to climate change (the MONARCH project)* (ed. P.A. Harrison et al.), pp. 241–256. Oxford: UKCIP Technical Report.
- Hayward, P., Nelson-Smith, T. & Shields, C., 1996. *Collins pocket guide to the seashore of Britain and Europe*. London: Harper Collins Publishers Ltd.
- Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.
- Inouye, D.W., Barr, B., Armitage, K.B. & Inouye, B.D., 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 1630–1633.
- Intergovernmental Panel on Climate Change, 2001. *Climate change 2001: the scientific basis. Contribution of working group I to the third assessment report of the Intergovernmental Panel on Climate Change* (ed. J.T. Houghton et al.). Cambridge: Cambridge University Press.
- Lawson, J., Davenport, J. & Whitaker, A., 2004. Barnacle distribution in Lough Hyne Marine Nature Reserve: a new baseline and an account of invasion by the introduced Australasian species *Elminius modestus* Darwin. *Estuarine, Coastal and Shelf Science*, **60**, 729–735.
- Lesica, P. & Steele, B.M., 1996. A method for monitoring long-term population trends: an example using rare Arctic–Alpine plants. *Ecological Applications*, **6**, 879–887.
- Lewis, J.R., 1964. *The ecology of rocky shores*. London: The English Universities Press Ltd.
- Lewis, J.R., 1986. Latitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral molluscs and cirripedes. *Hydrobiologia*, **142**, 1–13.
- Lewis, J.R., 1996. Coastal benthos and global warming: strategies and problems. *Marine Pollution Bulletin*, **32**, 698–700.
- Makarov, M., 1999. Influence of ultraviolet radiation on the growth of the dominant macroalgae of the Barents Sea. *Chemosphere: Global Change Science*, **1**, 461–467.
- McCarty, J.P., 2001. Ecological consequences of recent climate change. *Conservation Biology*, **15**, 320–331.
- Menge, B.A. & Branch, G.M., 2001. Rocky intertidal communities. In *Marine community ecology* (ed. M.D. Bertness et al.), pp. 221–251. Sunderland, MA: Sinauer.
- Michler, T., Aguilera, J., Hanelt, D., Bischof, K. & Wiencke, C., 2002. Long-term effects of the ultraviolet radiation on growth and photosynthetic performance of polar and cold-temperate macroalgae. *Marine Biology*, **140**, 1117–1127.
- Occhipinti-Ambrogi, A. & Savini, D., 2003. Biological invasions as a component of global change in stressed marine ecosystems. *Marine Pollution Bulletin*, **46**, 542–551.
- O’Riordan, R., 1996. The current status and distribution of the Australian barnacle *Elminius modestus* Darwin in Ireland. In *Irish Marine Science 1995* (ed B.F. Keegan and R. O’Connor), pp. 207–218. Galway: Galway University Press Ltd.
- Parmesan, C., 1996. Climate and species’ range. *Nature, London*, **382**, 765–766.
- Parmesan, C. et al., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature, London*, **399**, 579–583.
- Parmesan, C. & Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature, London*, **421**, 37–42.
- Pearson, T.H., Josefson, A.B. & Rosenberg, R., 1985. Petersen’s benthic stations revisited. I. Is the Kattegatt becoming Eutrophic? *Journal of Experimental Marine Biology and Ecology*, **92**, 157–206.
- Post, E., Peterson, R.O., Stenseth, N.-C. & McLaren, B.E., 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature, London*, **401**, 905–907.
- Post, E., Stenseth, N.-C., Langvatn, R. & Fromentin, J.-M., 1997. Global climate change and phenotypic variation among red deer cohorts. *Proceedings of the Royal Society, B*, **264**, 1317–1324.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. *Nature, London*, **421**, 57–60.
- Sagarin, R.D., Barry, J.P., Gilman, S.E. & Baxter, C.H., 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs*, **69**, 465–490.
- Sagarin, R.D. & Gaines, S.D., 2002. Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography*, **29**, 985–997.
- Shindell, D.T., Rind, D. & Lonergan, P., 1998. Increased polar stratospheric ozone losses and delayed eventual recovery owing to increasing greenhouse-gas concentrations. *Nature, London*, **392**, 589–592.
- Silva, P.C., 1955. The dichotomous species of *Codium* in Britain. *Journal of the Marine Biological Association of the United Kingdom*, **34**, 565–577.
- Southward, A.J., 1991. Forty years of change in species composition and population density of barnacles on a rocky shore near Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 495–513.
- Southward, A.J. & Crisp, D.J., 1954. The distribution of certain intertidal animals around the Irish coast. *Proceedings of the Royal Irish Academy B*, **57**, 1–29.
- Southward, A.J., Hawkins, S.J. & Burrows, M.T., 1995. Seventy years’ observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*, **20**, 127–155.
- Southward, A.J. & Southward, E., 1975. Endangered urchins. *New Scientist*, **66**, 70–72.
- Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B. & Osman, R.W., 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 15 497–15 500.
- Sweeney, J. & Fealy, R., 2002. A preliminary investigation of future climate scenarios for Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy B*, **102**, 121–128.
- Trowbridge, C.D., 2001. Coexistence of introduced and native congeneric algae: *Codium fragile* and *C. tomentosum* on Irish rocky intertidal shores. *Journal of the Marine Biological Association of the United Kingdom*, **81**, 931–937.

- Verling, E., Crook, A.C. & Barnes, D.K.A., 2002. Covering behaviour in *Paracentrotus lividus*: is light important? *Marine Biology*, **140**, 391–396.
- Visser, M.E., Noordwijk, A.J. van, Tinbergen, J.M. & Lessells, C.M., 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society, B*, **265**, 1867–1870.
- Walther, G.R. et al., 2002. Ecological responses to recent climate change. *Nature, London*, **416**, 389–395.
- Westholt, R., Kestler, P., Siken, O. & Westheide, W., 1999. Influence of sublethal long-term UV irradiation on body mass, reproduction and behaviour of north European *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 415–424.
- Wuethrich, B., 2000. How climate change alters rhythms of the wild. *Science, New York*, **287**, 793–795.

*Submitted 4 February 2005. Accepted 12 September 2005.*