Mar Biol (2010) 157:91–97
DOI 10.1007/s00227-009-1298-7

ORIGINAL PAPER

# Strengthening recruitment of exploited scallops *Pecten maximus* with ocean warming

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Received: 12 June 2009 / Accepted: 1 September 2009 / Published online: 16 September 2009


**Abstract** There is evidence that ocean warming has effects on the ecology, including recruitment dynamics, of marine organisms. In association with rising mean spring temperatures in the Irish Sea, a time-series of juvenile scallop *Pecten maximus* density around the Isle of Man showed a significant increasing trend since 1991. Favorable conditions (warmer water and correspondingly greater food availability) during gonad development can increase scallop gamete production. We examined the possibility that ocean warming has directly increased recruitment of exploited *P. maximus* around the Isle of Man by enhancing gonad development. From 1991–2007, there was a significant positive correlation between scallop recruitment and mean spring (the main period of gonad development) temperature in the year of larval settlement. Detrended (i.e., accounting for a time effect) recruitment data showed a marginally non-significant correlation to temperature. Gonadal somatic index of adult scallops and temperature were positively correlated. These relationships support the hypothesis that greater gamete production associated with ocean warming may be primarily responsible for observed increases in recruitment success and CPUE in a commercially important shellfish stock.

Communicated by S. D. Connell.

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## Introduction

There is developing evidence that ocean warming can have significant impacts upon the distribution and life history of many marine species. Distribution effects include range shift (Crisp 1964; Williams 1964; Perry et al. 2005; Hiddink and ter Hofstede 2008) or expansion (Zeidberg and Robison 2007) with some species at the latitudinal limit of their range showing reduced fitness (e.g., Kendall and Lewis 1986). Effects on key life history events seem to occur in many species: warmer years have been associated with earlier migration of squid to the English Channel (Sims et al. 2001), changing breeding date in tufted penguins (Gjerdrum et al. 2003) and shifts in recruitment dynamics of barnacles (Southward 1991; Lindley 1998; Herbert et al. 2003) and fin-fish including cod (Ottersen et al. 1994) and sprat (Mackenzie and Koster 2004). Recruitment shifts have been attributed to temperature-related changes in feeding, gonad development, or larval survival and may be more likely in species where recruitment is closely tied to climate-driven environmental variables.

This association between environment, physiology, and recruitment is exemplified by certain bivalve shellfish in which recruitment can be affected by climatic events at varying temporal scales (Powell and Mann 2005; Riasco 2006; Honkoop et al. 1998). Since shellfish are essentially sedentary, local changes in temperature or food availability are expressed physiologically, e.g., in metabolic rate, growth, or gonad development. This close connection between environment and physiology may be particularly important for scallops, in which inter-annual variation in production is attributed more to differences in gonad size (gamete production) than somatic growth; in effect, a year of 'good' environmental conditions will mean enhanced gonad development rather than larger scallops (MacDonald and Thompson 1985b). It is spring (northern hemisphere) conditions that may define a 'good' year as scallop gonad growth coincides with increasing water temperatures and phytoplankton production at this time (e.g., Sastry 1963) and favorable conditions maximize the contribution of vitellogenic oocytes in the scallop gonad (Saout et al. 1999). Correspondingly, many scallop species have shown greater gonad size in years of warmer water and an associated phytoplankton bloom in spring (MacDonald and Thompson 1985a, b; Robinson and Martin 2003; Wolff 1988). Gonad size and corresponding egg production have been directly correlated with recruitment in scallops (McGarvey et al. 1993); although, Slater (2005) found no correlation between gonad size and numbers of spat on artificial collectors. The complete connection between temperature, reproductive effort, and recruitment in scallops has been made occasionally (e.g., Claereboudt and Himmelman 1996) and suggests that a warming ocean might enhance scallop recruitment success.

Potential increases in scallop recruitment are currently of interest in Europe, where declining stocks of demersal fin-fishes have rendered commercial fisheries for scallop of rapidly increasing importance. In the UK, great scallops *Pecten maximus* currently represent the third most valuable fishery after prawns (*Nephrops norvegicus*) and mackerel (*Scomber scombrus*), and were worth over £34 million at first sale in 2005. Some scallop fisheries may be sustainable with effort control under current environmental conditions. However, many populations are increasingly heavily exploited and fisheries can depend largely on the strength of each recruiting year-class (e.g., Beukers-Stewart et al. 2003). This situation creates ongoing vulnerability to a single year of recruitment failure, especially since reproductive output in scallops is typically variable (Vahl 1982; MacDonald and Thompson 1985a, b; Wolff 1988). The effects of systematic or stochastic environmental change on recruitment success are thus extremely important. A similar situation exists in fisheries for American lobster *Homarus americanus* in Maine, USA where catches have been maintained at high levels of effort (Steneck and Wilson 2001) but recruitment likely depends on a small and potentially vulnerable component of the population (Ennis and Fogarty 1997). In exploited scallop stocks, negative environmental affects can be compounded by fishing activity (particularly dredging). Gonad development in non-captured scallops can be compromised because metabolic energy is diverted to repairing shell damage caused by physical impacts from fishing gear (Blythe-Skyrme et al. 2007).

Water temperature is well known to affect the dynamics of shellfish populations, particularly by influencing gonad development. Hence, ocean warming may have a significant positive effect on important commercial scallop fisheries for which it can be shown that a physiological response to temperature is linked to increased reproductive output. To test this hypothesis and to develop understanding of the process, we examined multi-year time-series of scallop gonad development, scallop recruitment, and environmental variables around the Isle of Man, and standardized scallop catch by UK vessels.

## Data collection

### Scallop survey data

For 20 years, the relative density (mean #/survey tow) of scallops of age-2 (juveniles) and ages ≥3 (adults) by fishing ground by year has been collected for Isle of Man fisheries. The scallop survey replicates 3–4 standard tows of defined position on each of 4–8 grounds. Four dredges are towed on either side of a beam-trawl vessel, with great scallop mesh/rings (80 mm internal diameter) used on one side and smaller (55 mm) 'queenie' (*Aequipecten opercularis*) mesh/rings on the other (Beukers-Stewart et al. 2003). The smaller mesh/rings of the queenie gear are more fully selective for age-2 scallops and thus provide a reliable and consistent index of relative density of juveniles. Surveys of scallop recruitment at earlier life history stages are impractical due to difficulties in capturing and counting shellfish in a reproducible manner at larval or newly settled stages. Annual relative density of age-2 scallops has fluctuated sufficiently through the survey period that given year classes may be followed through multi-annual length-frequency distributions for the population. This has resulted in a well-established relationship between the relative density of age-2 and each of age-3 ($R^2 = 0.85$) and age-4 ($R^2 = 0.73$) scallops (Beukers-Stewart et al. 2003). Greater densities of age-2 scallops anticipate a larger population of exploitable adults 1–3 years later.

Mean number of adult and age-2 scallops survey tow$^{-1}$ year$^{-1}$ was calculated for each of eight survey grounds for 1991–2005 and 2007. There were some missing data as certain grounds were not surveyed every year. Missing data were imputed using the multiple imputation routine in the Amelia II package in R (Honaker et al. 2006). This routine filled in sampling gaps so that subsequent analyses could use all the information present in the dataset and avoid the bias associated with missing values. Five possible complete sets of each of adult and age-2 data by ground by year were calculated. From these sets, five corresponding overall annual mean numbers of each of adult and age-2 scallops/survey tow by year were then calculated.

### Environmental data

In addition to the scallop fisheries survey data, two multi-annual time series of marine water quality data exist for the sea area around the Isle of Man. The CYPRIS sampling site on the west coast of the Isle of Man has been studied for over 50 years and cited in numerous scientific studies (e.g., Allen et al. 1998; Evans et al. 2003). In summer, the water column at the CYPRIS station is transitional in character, being positioned just inshore of the main western stratified water mass and offshore of true coastal waters (Pingree and Griffiths 1978). Conversely, the RESA site is located on the east coast of the Island in an area of well-mixed and faster flowing water (Bowers et al. 1998). Water temperature, oxygen concentration, and chlorophyll *a* variables were derived from the CYPRIS (1989–2005) and RESA (1994–2003) datasets of water quality (each of surface and seabed); although, CYPRIS data from 1990 were excluded as they were incomplete. As with recruitment, missing data were imputed using Amelia II (Honaker et al. 2006). This produced five possible complete datasets (each dataset comprising a full time series for each of CYPRIS and RESA at surface and seabed) for each variable.

### Scallop landings

Records (1994–2005) of international landings of *P. maximus* (UK vessels) were obtained from CEFAS. These data were standardized for engine power and regression analysis used to test for possible trends.

## Analysis

### Correlating scallop recruitment and environmental variables

A single annual value (mean #/survey tow) for juvenile scallops (recruitment—R) was calculated by averaging the five imputed sets of annual means. The overall R time-series was normally distributed [Lilliefors test with acceptable skewness ($\alpha = 0.05$, $n = 15$y) being $\pm 1.040$] and showed no autocorrelation by time (year).

Single annual values for each environmental variable were also calculated. A primary principal component was derived (using PCA) for each of the five imputed data sets. For each of the five imputed datasets, this principal component captured dominant environmental trends across all four sampling stations. The five principal components of each environmental variable then were averaged by year to provide an overall proxy.

Proxy environmental variables were related to the scallop survey data in order to determine possible climate (temperature) effects on recruitment and to understand the possible confounding or interacting influences of other key environmental factors. The R series (with a 2-year lag) was plotted against the temperature proxy for visual assessment (Fig. 1). Recruitment (R) then was related to this series and to the other proxy environmental variables (oxygen concentration and chlorophyll *a*) using step-wise multiple linear regressions (MLR) (variables rejected at $P = 0.1$). In all cases, environmental variables were related to R 2 years later. All regressions were tested for linearity and equal variance of variables by examination of residual plots.

### Possible spawning stock influences on scallop recruitment

Within the context of a fluctuating environment, recruitment of marine species is often related to spawner abundance (Myers and Barrowman 1996) and if this is the case, adult stock size (SS) must usually be accounted for in studies that relate recruitment to climate indices (Cardinale and Hjelm 2006). To test for an SS–R relationship, R was related to SS (# adults/survey tow 2 years earlier) using each of linear and quadratic models.

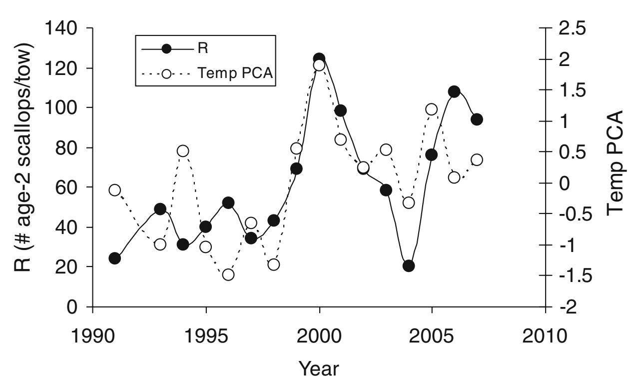


**Fig. 1** Time series of mean spring sea temperature (a principal component derived from four time series of water temperature–CYPRIS 0 m and 37 m and RESA 0 m and 36 m) and scallop recruitment (R) 2 years later

Effects of long-term trends in R and temperature data

Since both recruitment and temperature data showed long-term positive trends, there was a danger of spurious correlation between the two series. This possibility was mitigated by the large inter-annual variability in both series. However, the use of residuals provides additional weight to analyses of climate/environment effects on long-term biological time series by effectively de-trending the data (Votier et al. 2007). Residuals were derived from a linear regression of R against year ($n = 16$; $R^2 = 0.335$; $P = 0.019$). These residuals then were regressed against the temperature proxy, being the only significant environmental variable produced from regressions (above), to see if temperature also accounted for anomalies in the dominant recruitment trend.

Does warmer water drive recruitment by enhancing scallop gonad size?

To test the hypothesis that recruitment is driven by a positive effect of temperature, on gonad development rather than simply showing a spurious correlation or a correlation with time (see also above), it was necessary to use actual time series of scallop gonad state. It is established that Isle of Man scallops have two annual spawning events (summer and autumn) with the summer event contributing most to total annual recruitment (Andrew Brand, unpublished data). Gonad data from spring (pertaining to the important summer spawning) were not available, but a 5-year time series of scallop gonadal somatic indices (GSI) were available for July (2001–2002) and August (2003–2005), i.e., pertaining to the autumn spawning. These two datasets ($N = 5$ data points) were related to mean water temperature (CYPRIS 0 m) during the previous 3 months (the period of gonad development equivalent to spring) using ANCOVA with month as a categorical variable and temperature as a covariate (continuous variable). The interaction between temperature and month was tested.

## Results

International landings of scallops by UK vessels showed a significant increasing trend from 0.000331 t/kW in 1994 to 0.000525 t/kW in 2005 ($R^2 = 0.662$, $P = 0.002$, $F_{11} = 16.483$). Examination of temporal trends in the longest raw data series (CYPRIS) showed a significant increasing trend in mean spring seabed temperature ($n = 15$, $R^2 = 0.32$, $P = 0.029$). The proxy temperature series showed a marginally non-significant increasing trend ($n = 13$, $R^2 = 0.294$, $P = 0.056$) for 1993–2005 (Fig. 1). The annual mean number of juvenile scallops/survey tow (1991–2007) (R) also showed a significant increasing trend ($n = 16$; $R^2 = 0.335$; $P = 0.019$). Both linear ($P = 0.277$, $R^2 = 0.090$) and quadratic ($P = 0.129$; $R^2 = 0.289$, $F_{12} = 1.94$) (Fig. 2) models suggested only a weak effect of SS on R, highlighting potential for the dominance of environmental effects on recruitment success.

From the three tested environmental variables, MLR models of scallop recruitment retained only mean spring temperature as a possible explanatory variable. The principal component proxy for mean spring temperature was related significantly to R ($n = 16$, $R^2 = 0.394$, $P = 0.009$) (Fig. 3). A correlation between residuals from a linear regression of scallop recruitment R against year, and the temperature proxy, approached significance ($n = 16$, $R^2 = 0.203$, $P = 0.080$) (Fig. 4).

Scallop GSI (indicating relative gonad development) was greater when mean water temperature for the 3 months prior to sampling (the period of gonad development) was greater. An ANCOVA with month as a categorical variable and temperature as a covariate (continuous variable)

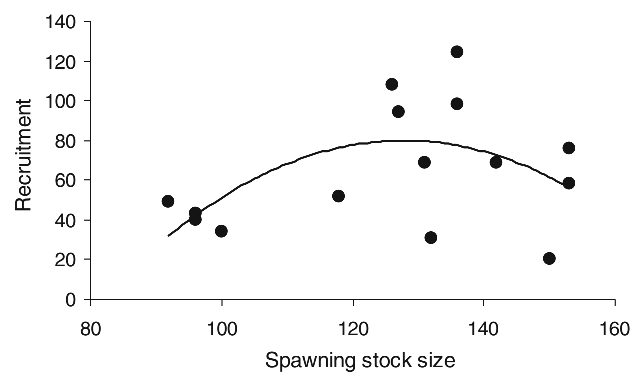


**Fig. 2** Quadratic model of Isle of Man scallop spawning stock size (SS) and recruitment (R = number of age-2 scallops 2 years later)

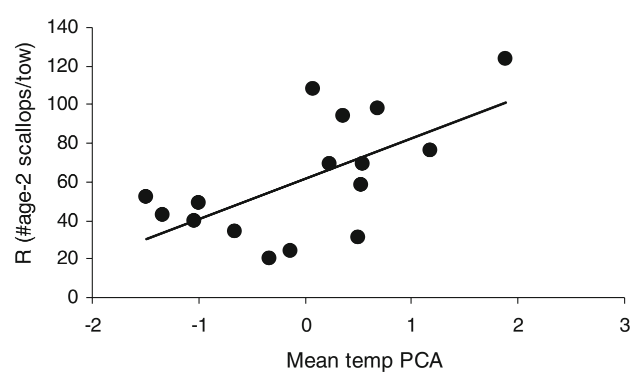


**Fig. 3** Significant linear relationship between Isle of Man scallop recruitment R and a proxy (a principal component derived from four time series of water temperature—CYPRIS 0 and 37 m and RESA 0 and 36 m) for mean spring (MAM) sea water temperature (°C) 2 years earlier

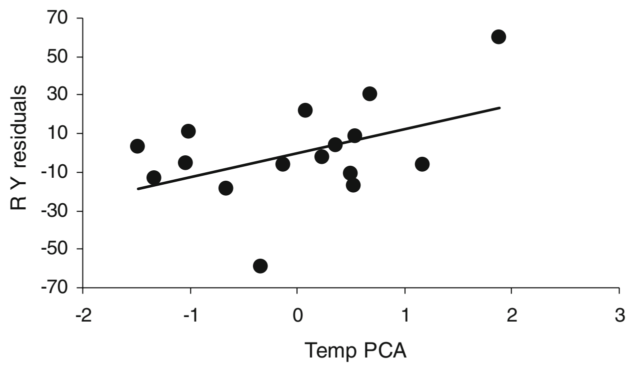


**Fig. 4** Linear relationship between the residuals of a regression between Isle of Man scallop recruitment R and year (1991–2007) Y, and a proxy for mean spring (MAM) sea water temperature (°C) 2 years earlier (a principal component derived from four time series of water temperature—CYPRIS 0 and 37 m and RESA 0 and 36 m)

showed a marginally non-significant effect of temperature on GSI ($R^2 = 0.887$, $P = 0.069$, $F = 10.084$) and no effect of month ($P = 0.109$, $F = 2.689$). The interaction between temperature and month was not significant ($P = 0.780$).

## Discussion

For the Isle of Man, a proxy time-series (1991–2007) of spring mean water temperature showed a significant positive correlation with scallop recruitment (number of age-2 scallops) 2 years later. In common with many scallop populations, spring is the main period of gonad development for Isle of Man *P. maximus*. Hence, we tested the hypothesis that warmer water during development enhances gonad size, a measure of reproductive potential. The Isle of Man falls around the middle of the latitudinal range for *P. maximus*, which extends from northern Norway to North Africa (Brand 2006). Thus, increasing water temperature in association with adequate food supply could directly explain increasing scallop recruitment via a gonad development mechanism. Accordingly, a limited available (5 year) dataset suggested that scallop gonadal somatic index (GSI) for Isle of Man scallops was greater in years showing a warmer spring. This conforms to many prior observations of a positive effect of spring temperature on shellfish gonad development (e.g., MacDonald and Thompson 1985a, b; Robinson and Martin, 2003; Wolff 1988), gamete production (e.g., Saout et al. 1999), and recruitment (Claereboudt and Himmelman 1996) and suggests that ocean warming is likely to be primarily responsible for observed increases in recruitment and in commercial CPUE from an exploited scallop population.

None the less, while the current study found a compelling positive relationship between spring temperature and both gonad development and recruitment success, this is not the conclusive evidence of the proposed gonad development mechanism. Although enhanced gonad development typically results in greater gamete production, this does not necessarily translate into greater competency of larvae. It is possible that warmer water is positively effecting scallop recruitment by increasing larval survival or settlement. However, the key outcome is the same: the current warming trend in spring ocean temperature correlates with more juveniles recruiting to the adult population and thus growing stocks of exploited scallops.

A possible confounding factor in this interpretation is the warming trend in ocean temperature around the Isle of Man, i.e., time and temperature are correlated significantly. Such a trend might produce spurious correlations if scallop recruitment (and commercial CPUE) had increased over time for some other (non-temperature) reason. The possibility of a spurious correlation is countered in our data by both (a) the residual analysis described above, which shows a marginally non-significant relationship between temperature and detrended recruitment data, and (b) by the observed positive relationship between temperature and scallop GSI.

Other potential effects on recruitment could include different environmental factors or significant new fisheries management measures. Since we also tested for relationships between scallop recruitment and each of oxygen concentration (ml/l) and chlorophyll *a* concentration (μg/l), these key environmental factors can be rejected. Concerning fisheries management, the Isle of Man has introduced some local effort control measures during the past 5 years, but not at the time-scale of observed increases in scallop recruitment. A longer-term management tool has been maintenance of a small area of seabed closed to fishing. Scallop density within this closed area has increased markedly in recent years but there is not yet conclusive evidence that the area exports spat to other local scallop beds. Oceanographic currents make it unlikely that spat from such an area on the SW Isle of Man would contribute to grounds to the north and east of the island where recruitment increases similar to those on grounds adjoining the closed area were observed. In addition, the closed area does not impact at the national or EU scale that would be necessary to explain significant increases in commercial CPUE by the UK fleet shown in this study.

Links have previously been made between water temperature and recruitment in a number of scallop species. These studies have typically been short-term (<3 years) or experimental, but suggest that the combination of planktonic food availability for larvae, and temperature influences on metabolism of adults, represents likely mechanisms for the multi-annual relationships that we observed. There is additional evidence that relatively warmer water and associated phytoplankton blooms might directly benefit adult scallops in the period approaching spawning. Notably, the Irish Sea experiences a spring phytoplankton bloom from around April–May (Gowen et al. 1995; Trimmer et al. 1999), corresponding to the important temperature period observed in our study. Lawrence (1993) has found that this is the only time of year when phytoplankton, as opposed to benthic diatoms, predominate in the diet of Isle of Man *P. maximus* suggesting that energetic intake during spring relies on a food source that is explicitly temperature mediated.

The maintenance food requirement for scallops increases with temperature (Heilmayer et al. 2004) such that warmer water in the absence of excess food would have a negative effect on growth and reproductive development (Pilditch and Grant 1999). This could be important if greater winter temperatures increased scallop metabolism outside the season of light-driven phytoplankton blooms. However, because metabolism increases, *P. maximus* can consume a greater food ration (if available) as temperature increases from 8.0°C upward (equating to the lower end of the range of mean spring temperatures that we observed), with growth rate increasing correspondingly (Laing 2000). Hence, in a warmer spring, scallops *can* consume more at just the time when the phytoplankton bloom supplies its annual high-energy food bonanza and winter mixing of the water column transports this nutrient pulse to the benthos. Thus, energy assimilation by scallops may be greatest in warmer springs and thus directly enhance reproductive potential (gonad size) in spawning adults. This would translate into stronger year classes of age-2 scallops 2 years later (as observed in the present study) and greater recruitment to the fishery in the subsequent 2 years (explaining observed increases in commercial CPUE).

In addition to, and interacting with, the effects of ocean environment and SS, community level factors such as predation may significantly influence shellfish recruitment (e.g., Philipart et al. 2003). In the Mid-Atlantic Bight, recruitment of sea scallops was significantly lower in areas showing relatively high abundance of *Asterias* spp. (Hart 2006). Importantly, this relationship is often temperature dependent with population density and predation by sea stars (Barbeau et al. 1994; Sanford 1999) and *Crangon crangon* (Strasser and Gunther, 2001; Beukema et al. 2004) greater in warmer years. Such a positive temperature effect implies that warmer spring temperatures around the Isle of Man would likely results in greater densities of both scallops and their key predators. Other mechanisms also apply. In a large scale community study in the Gulf of Maine (Witman et al. 2003), it was shown that density of *Asterias* spp. had a bottom-up connection to density of shellfish prey with sea star density increasing significantly in the 10–23 months following a large prey recruitment event. According to this observation, peaks in sea star predation are likely subsequent to peaks in scallop recruitment that may be primarily driven by other (environmental) factors, and probably cycle at a different temporal scale. While predation likely exerts a dampening effect on recruitment of scallops around the Isle of Man, this effect appears insufficient to mask dominant climate (e.g., water temperature) driven recruitment anomalies. Such abiotic anomalies still extend beyond the biological characteristics (including predation) of the SS–R relationship and sustain the argument that recruitment of Manx scallops is positively effected by rising sea temperature.

In addition to environmental and community effects, fishing can also impact scallop recruitment. Given the current rapid increase in scallop fishing effort, major management developments may be required. Of relevance here are observations of reduced recruitment in heavily fished scallop populations (Blythe-Skyrme et al. 2007) and negative impacts of fishing on aspects of the benthic community (e.g., Kaiser et al. 2000). Both these potential problems might be addressed by marine-protected areas having a large biomass of adult scallops. Such areas would maintain a biodiverse seafloor community and harbor a reservoir of highly fecund individuals that could act as producers of scallop spat to the broader fishery.

**Acknowledgments** The authors thank Theresa Shammon for advice on the CYPRIS and RESA datasets. Tom Bryan-Brown (MFPO) and Andy Read (DAFF) provided logistical support and local knowledge. This work was carried out through funding to M. J. Kaiser (University of Bangor) from the Isle of Man DAFF.

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