

RELATION BETWEEN WATER QUALITY AND DORSAL THICKNESS OF MUSSEL (*MYTILUS EDULIS*) AND ITS ECOLOGICAL IMPLICATIONS FOR WINTERING OYSTERCATCHERS (*HAEMATOPUS OSTRALEGUS*)

NAGARAJAN, R.^{1,2}, LEA, S.E.G.¹ and GOSS-CUSTARD, J. D.³

¹*School of Psychology, Washington Singer Laboratories, Perry Road, University of Exeter Exeter EX4 4QG, UK; E-mail: R.Nagarajan@ex.ac.uk*

²*PG and Research Department of Zoology, Wildlife Biology and Biotechnology A.V.C. College, Mannampandal–609305, Tamilnadu, India*

³*Havering, Church Road, Lympstone, Devon, EX8 5JT, UK*

The Individual Behaviour Based Model developed using Oystercatchers (*Haematopus ostralegus*) as a model species is successful in predicting the impacts of environmental changes in aquatic ecosystems. At its heart is a food depletion model which assumes that consumers will tend to starve in highly depleted areas and seasons. Since dorsal hammering Oystercatchers selectively deplete dorsally thin-shelled mussels (*Mytilus edulis*), we measured the dorsal thickness of the shells of small (34–46 mm), medium (44–46 mm) and large (54–56 mm) length classes and assessed the water quality across the seasons (September to March) in the Exe estuary, Southwest England. Water temperature decreased across the season from autumn whereas salinity increased until late October and then decreased during rest of the season. In parallel, mussel shell thickness decreased until mid-winter and then started to increase. This increase could be associated with the Oystercatchers' selective predation on thin-shelled mussels. Multiple regressions confirmed that the changes in the salinity across the season were associated with the overall thickness variations of the shells. We conclude that salinity had a significant influence on the thickness variations of medium and large classes of mussels, and water temperature significantly influenced the dorsal thickness of large mussels. Changes in water quality did not significantly influence small mussels. Our result suggests that, despite the selective removal of significant numbers of thinner-shelled mussels by Oystercatchers, the density of thin-shelled prey available to them may increase because of changes in the salinity and water temperature.

Key words: mussel thickness, Oystercatchers, salinity, water temperature, wintering season

INTRODUCTION

Considerations of water quality are important in waterbird habitat evaluation because a host of interacting physical and chemical factors can influence the level of primary productivity in aquatic systems and thus influence the trophic structure and total biomass throughout the aquatic food web (WETZEL 1975). A relationship between water quality and waterbirds had already been indicated by several studies (e.g. PATTERSON 1976, MURPHY *et al.* 1984). Physiochemical characteristics of the water largely determine the waterbird community of aquatic habitats, pri-

marily by their direct and indirect impact on the availability and abundance of the birds' prey (e.g. NAGARAJAN & THIYAGESAN 1996). Furthermore the undesirable changes in the water quality due to developmental activities such as industrialisation, urbanisation, construction of roads and dams, intensification of agriculture, expansion of aquaculture and eco-tourism alter the habitat utilization of waterbirds and are often used as indicators of water quality (e.g. FECK & HALL 2004, NAGARAJAN & THIYAGESAN 2006).

Water quality influences the availability and accessibility of prey items to various aquatic predators (e.g. NAGARAJAN & THIYAGESAN 1996, 1998). Often temperature is known to influence the life of aquatic organisms (ODUM 1983). For example, increasing temperature positively influences the growth and survival of aquatic organisms (e.g. ALDRIDGE *et al.* 1995). Furthermore MCGOWAN *et al.* (2002) showed that an increase in the mud temperature increases the foraging success of red knots, *Calidris canutus*, whereas SMITH and EVANS (1973) inferred that a temperature decrease towards 0 °C makes lugworms become less active and move to the surface less often, which had a negative influence on prey capture by bar-tailed godwits, *Limosa lapponica*. Hence temperature plays an important role in the aquatic organisms' survival, growth, population, availability, and accessibility.

Salinity plays a vital role in aquatic environments, especially in variably saline habitats such as estuaries and coastal areas. Organisms which live in a saline environment are sensitive to changes in its salinity (e.g. NAGARAJAN *et al.* 2006). WESTERBOM *et al.* (2002) investigated the distribution of mussels in relation to salinity gradient in the northeastern Baltic Sea and found a marked decline in mussel size and biomass from the saline west to the less saline east. They also found that a long period of low salinity negatively affected the growth of population of mussels. On the Exe estuary, salinity rapidly declines towards the upstream part of the estuary, where no mussel beds are established (MURRAY 1980). Salinity also influences the quality of aquatic organisms through physiological changes. For example, a decrease in salinity increases the valve closure period of bivalves, which makes them utilize stored energy and undertake the undesirable mode of anaerobic respiration (AKBERALI *et al.* 1983). All this empirical evidence suggests that temperature and salinity are two prime water quality variables which influence the mode of aquatic organisms. Also NAGARAJAN *et al.* (2006) speculated that the seasonal variations in the shell thickness could be associated with the changes in the water temperature and salinity during winter. Hence in this paper we investigate the effect of water temperature and salinity on the dorsal thickness of mussels on the Exe estuary across the seasons.

MATERIALS AND METHODS

Study area

The river Exe in Devon forms a ria (submergent coastal land), mainly muddy, sheltered estuary which is in the Southwest of England between Exmouth and Dawlish to the west (Fig. 1). The estuary is protected from the sea by twin sand spits which reduce the entrance to a narrow channel (MCGRORTY 1997). The main supply of freshwater comes from the rivers Exe and Clyst which enter from the north. BOALCH (1980) has summarised the details and descriptions of geology, hydrography, sedimentology, fauna, and flora of the Exe.

Thirty-one mussel beds were recognised during 1976 when the Institute of Terrestrial Ecology began a long term investigation of Oystercatcher populations and foraging behaviour aiming to identify and quantify factors that determine the number of birds that an estuary can support and the impact they have on the prey population (GOSS-CUSTARD *et al.* 1982). There are currently 10 main mussel

beds scattered throughout the seaward half of the estuary (Fig. 1), on which 80% of the birds that ate mussels occurred at the period of the research described here (DURELL & GOSS-CUSTARD 1996). The dominant species is the edible or blue mussel, *Mytilus edulis*, and the dense population of mussels forms the foundation for this area, much of the stability of the area probably being owed to the inter connection of molluscs by their byssus threads. The bottoms and lower sides of the channels and the pools which result from the periodical fragmentation of some of them are often thickly covered in accumulated mud or gravely sand (HARRIS 1980). Mussel bed number 4, which is located on the western side of the Exe estuary, between Starcross and Cockwood ($3^{\circ}27'W$, $50^{\circ}37'N$) was selected for this study (Fig. 1). The water temperature of estuary of Starcross area was lowest of $6^{\circ}C$ during February and highest of $18.4^{\circ}C$ during July and August and the salinity ranged from 10 ppt to 34 ppt between January and April (MURRAY 1980).

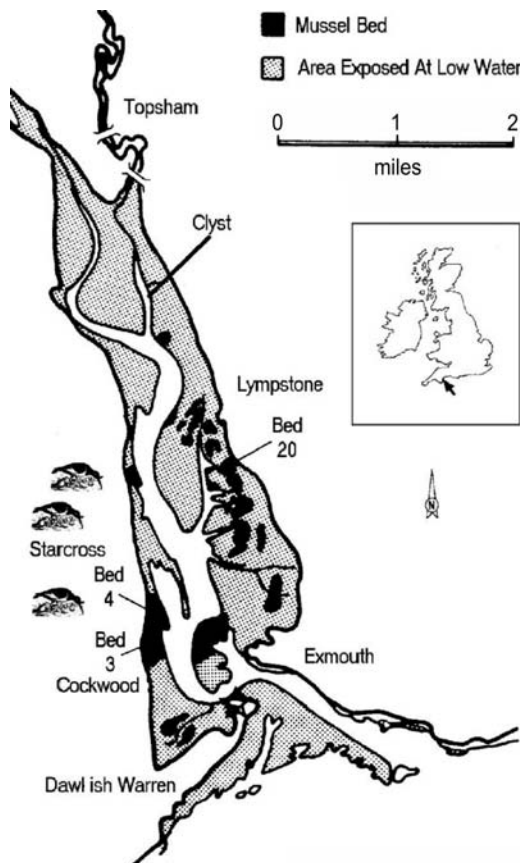


Fig. 1. The study area within the Exe estuary in south west England showing different mussel beds

Mussel collection

Approximately once a fortnight, towards the end of the low tidal cycle, 24 mussels of 3 different length classes i.e.

small 34–36 mm; medium 44–46 mm and large 54–56 mm (8 mussels per length class) were collected. Collection took place from August 2005 to March 2006, so as to monitor changes in the dorsal thickness of the mussels as per the method described in NAGARAJAN *et al.* (2002a, b).

Length

The length of the mussel from anterior tip (umbo) to posterior tip was measured using a vernier calliper accurate to 0.05 mm.

Dorsal thickness

The shell thickness at the centre of the scar where the adductor mussel attaches to the valve was measured using a Mitutoyo digimatic micrometer accurate to 0.001 mm.

Water quality

The salinity and temperature of the water on the mussel bed was measured whenever mussel collections were made. The salinity was measured using a refractometer with an accuracy of 1 ppt (SANT'ANNA *et al.* 2006). The temperature was measured using a mercury thermometer with an accuracy of 0.1 °C (NAGARAJAN & THIYAGESAN 1996). The measurements were made in 7–10 tidal pools of different places of mussel bed at low tide and in open water on the next incoming tide from the depth range of 5–10 cm, and the mean of these two measurements was taken.

Statistical analysis

Statistical analyses were performed by using window based statistical packages Minitab. Variations in mussel thickness could be due to differences in mussel length, as well as changes in season, water quality (water salinity and water temperature) and interactions between water quality variables. So the dorsal thickness of mussels was regressed against these variables in iterative stepwise multiple regression. The seasonal effect was investigated by including a variable indicating the number of days elapsed since 1 August (hereafter referred as “day”; NAGARAJAN *et al.* 2002c) in the analysis. We developed regression models using both step-up and step-down procedures. In all the regression models, assumptions about the nature of the data such as

- the relationship between the response variable (also called ‘dependent variable’) and predictor variable (independent variable) is linear;
- homogeneity of variance; the residuals in Y axis should not show a tendency to increase or decrease as X axis (Fits) increases, which is called ‘heteroscedasticity’ or ‘shotgun effect’ (WATT 1998);
- the residuals have normal distribution were tested.

To investigate relationship between the response and predictor variable, the raw data was plotted by using Minitab’s Lowess plot. If the figure showed a linear trend then the variable entered in the regression model in linear form, if it was a curve then both linear and quadratic form (square the variable) were used. In the step-up procedure, the first step was entering the most influential predictor variable in the model, then the residuals of that model were plotted against fits to explore the heteroscedasticity problem. We noticed heteroscedasticity problem, so the response variable (dorsal thick-

ness) was log-transformed and developed the model again which allowed us to overcome the heteroscedasticity problem and made the variability stable. If the variable was significant on its own then the second most important predictor variable was entered and the new equation was checked for heteroscedasticity problem. If the variable was significant on its own (t-test; co-efficient significantly different from zero) then the variable was retained in the model, otherwise was eliminated from the subsequent model, then the third predictor variable was entered and the above procedures were repeated. The same procedure was followed in each step and also in step-down model as well. The third assumption; normal distribution of residuals was tested using the histogram of residuals. At the end, the final refined model was derived with variables individually significant on its own. The final model was run with all the significant predictor variables without one predictor and this predictor was plotted against the residuals of the model to finally check the linear relationship between response and predictor variables. The same procedure was repeated for all other predictor variables (NAGARAJAN *et al.* 2002b).

RESULTS

Water quality

The water salinity of the mussel bed ranged from 17.3 ppt (7 December) to 30.6 ppt (16 September) across the season. It was highest during the early part of the season between 25 August and 4 October. The salinity was low during the rest of the season with three minor peaks (Fig. 2).

The water temperature on the mussel bed ranged from 5.7 °C (4 February) to 19.4 °C (1 September) for the season. The water temperature declined to 6.8 °C on 12 November and stayed almost constant during rest of the season (Fig. 2).

Dorsal thickness

Overall mean dorsal thickness was highest (mean±SE = 1.14±0.032 mm), on 1 September and declined to 0.99±0.027 mm on 7 December. Then the thickness increased slightly to 1.12±0.034 mm and then declined during the rest of the season (Fig. 2). The dorsal thickness of the small length class varied from 0.92±0.043 mm (21 November) to 1.10±0.062 mm (11 January), of the medium class from 0.90±0.115 mm (19 October) to 1.22±0.045 mm (1 September), and of the large class from 1.05±0.027 mm (7 December) to 1.26±0.059 mm (1 September) (Fig. 3).

Influence of water quality on the dorsal thickness

The influence of season and water quality variables on the dorsal thickness of mussels was investigated using multiple regression equation models. Since length has a predominant role on the dorsal thickness of the mussels, the effect of length

was controlled in all the models by including it as a variable (Table 1). The seasonal variable both day (linear) and day² (quadratic) were significant which indicated that the fluctuations in the dorsal thickness across the season was significant (Table 1; set 1). The water quality variables salinity and water temperature were entered in the regression equation which indicated that they did not significantly influence the dorsal thickness of mussels. When the interaction term between salinity and water temperature was included in the regression, this term showed highly significant influence on the dorsal thickness of the mussels (Table 1; set 2), whereas the effect of season became non-significant. The significance of the interaction term indicated that the combined effect of salinity and water temperature influenced the dorsal thickness of mussels significantly. With the interaction included, the main effect of salinity was significant and water temperature became marginally non-significant. When we dropped the water temperature in another regression, the salinity became non-significant. In addition, the effects were negative and small, which is uninterpretable, so the salinity and water temperature were dropped from the final model (Table 1; set 2). A hierarchical regression analysis indicated that the length of the mussels explained 23.4% of the total variation in the dorsal thickness of mussels. The subsequent inclusion of the interaction term between salinity and water temperature significantly increased the R^2 to 25.5%, whereas inclusion of the seasonal variable 'day' and the main effects of water quality variables did not increase R^2 significantly.

Individual regression equation on different length classes showed that the season as well as water quality did not have any effect on the dorsal thickness of small length class. The fluctuations in the dorsal thickness in the medium length class showed a significant quadratic relationship with the season (Table 2; set 1). The subsequent model including water quality variables (salinity and water temperature) and interaction between these two variables made the seasonal variable

Table 1. Regression equation models (overall data; irrespective of length class) on dorsal thickness of mussels (\log_{10}) to explore the effect of season and water quality.

Set	Independent variable group (n = 385)	Predictors	Coefficient \pm SE	P	Model (r^2)	Model (P)
1	With season only	Constant	-0.11804 \pm 0.01993	0.000	0.250	<0.001
		Length	0.0041 \pm 0.000371	0.000		
		Day	-0.000579 \pm 0.0002075	0.01		
		Day ²	0.00000191 \pm 0.00000083	0.05		
2	With water quality	Constant	-0.168 \pm 0.0178	0.001	0.254	<0.001
		Length	0.00411 \pm 0.0003711	0.001		
		Salinity \times water temperature	0.0000584 \pm 0.0000178	0.001		

non-significant. This model indicated that the variation in the dorsal thickness across the season was due to changes in and interactions between salinity and water temperature (Table 2; set 2). The changes in the dorsal thickness in the large length class showed a significant linear decrease across the season (Table 2; set 3).

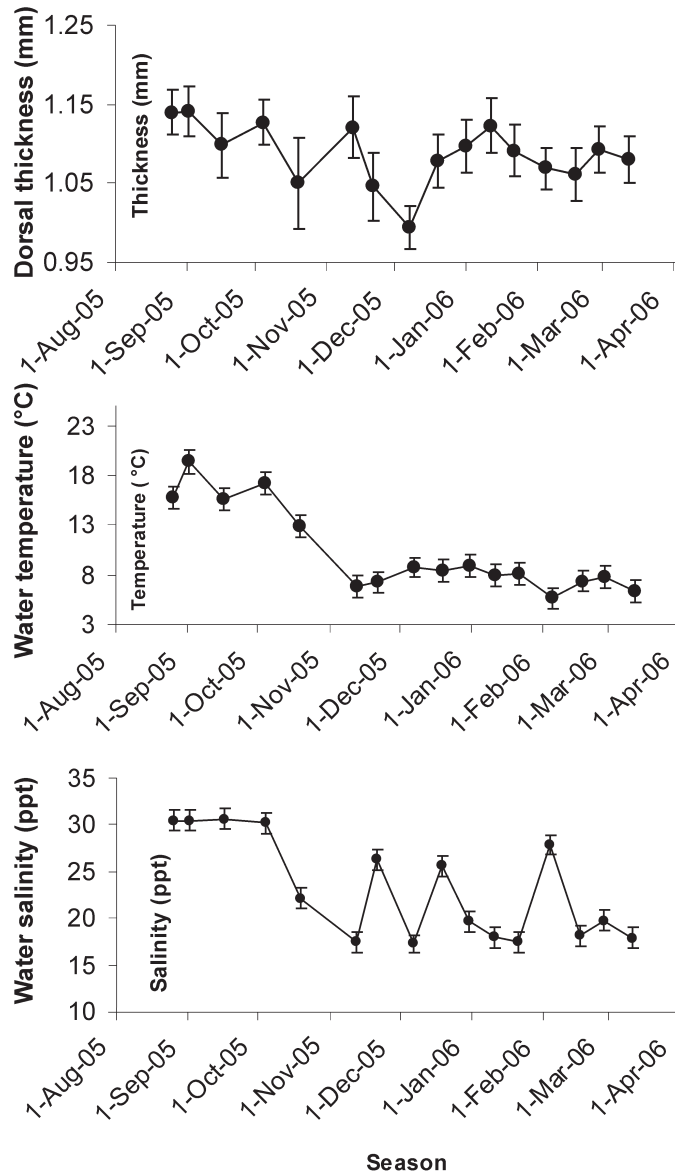


Fig. 2. Variations (Mean±SE) in dorsal thickness of mussels, water temperature and salinity across the season

The subsequent model including interaction between salinity and water temperature made the seasonal variable non-significant (Table 2; set 4). The water quality variable salinity and water temperature did not show any significance on its own in large length class. As expected, the length of the mussels did not show a significant

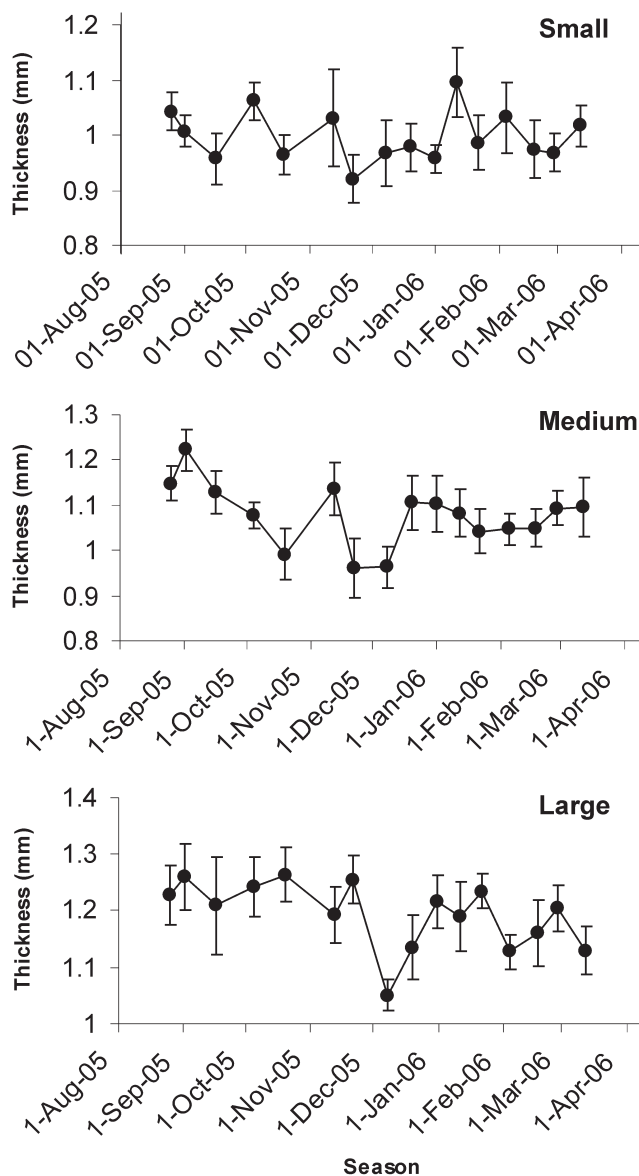


Fig. 3. Variations (Mean \pm SE) in dorsal thickness of mussels of different length classes across the season

Table 2. Regression equation models on dorsal thickness of medium and large lengths class mussels (\log_{10}) to explore the effect of season and water quality.

Set	Independent variable group	Predictors	Coefficient \pm SE	P	Model (r^2)	Model (P)
Medium length class ($n = 129$)						
1	With season only	Constant	0.09297 \pm 0.0204	0.000	0.078	<0.01
		Day	-0.0011626 \pm 0.0003742	0.01		
		Day ²	0.00000416 \pm 0.00000148	0.01		
2	With water quality	Constant	0.3242 \pm 0.1085	0.01	0.113	<0.01
		Salinity	-0.011642 \pm 0.004038	0.01		
		Water temperature	-0.03576 \pm 0.01256	0.01		
		Salinity \times water temperature	-0.00000001 \pm 0.00000001	0.01		
Large length class ($n = 128$)						
3	With season only	Constant	0.09376 \pm 0.0106	0.000	0.034	<0.05
		Day	-0.00015669 \pm 0.00000741	0.05		
4	With water quality	Constant	0.057725 \pm 0.008732	0.000	0.035	<0.05
		Salinity \times water temperature	0.00006294 \pm 0.0000293	0.05		

influence on the dorsal thickness within any length class, so the length was not entered in any of the length-wise regression models (Table 2).

DISCUSSION

We found that the significance of the seasonal variation on dorsal thickness of mussels became non-significant when water quality variables were entered in the regression models. The interaction between water salinity and temperature had strongly significant associations with the changes in the dorsal thickness of mussels. What would be the reason for the influence of the interaction between water salinity and temperature on shell thickness?

Given that there is no reproduction or replacement of mussels during the winter, any selective removal by Oystercatchers could only cause an increase in mean thickness. This result strongly suggests that shell thickness changed in individual mussels through the winter. Earlier we suspected that the change in the water temperature and salinity could cause changes in the mussel shell thickness and have discussed the possible evidence for such an effect and its likely mechanism (NAGARAJAN *et al.* 2006). Briefly, earlier studies (AKBERALI *et al.* 1977, 1983,

CRENSHAW & NEFF 1969, FOX & COE 1943, RAO & GOLDBERG 1954) suggested that the reduction of salinity due to increased freshwater flow inflicts stress on the mussels. Thus they close their valves and respire anaerobically, which yields the by-products of succinic acid and ammonia. To neutralise the metabolites, the mussels dissolve the calcium carbonate from their shells. The decrease in the water temperature which continues throughout winter affects the calcification processes (MEZQITA *et al.* 1999), an additional factor likely to cause thinning. The current result suggests that the seasonal changes in the water salinity and temperature were sufficient to cause the changes in the mussel shells across the season.

Water quality, both water temperature and salinity, had a significant influence on the large length class, but the medium length class was influenced by salinity alone and the small length class was not influenced by either temperature or salinity. The variations in the influence of water quality variables on the changes of dorsal thickness of different length classes of mussels could be associated with the location of individual mussels as a function of their age. There is a strong correlation between length and age of mussels (KAUTSKY 1982). On the mussel beds, the mussels form a cluster by attaching to each other and the substrate using the byssus thread. The spat always settle in the innermost area of the cluster to protect themselves from predators and therefore a gradation of age class can be seen in the cluster, with most of the larger mussels on the outer layer. Therefore the larger mussels are exposed most of the time to the varying water quality due to tidal waves and freshwater runoff. Such frequent exposure to varying water quality would give it a greater influence on larger mussels.

Ecological implications

Oystercatchers, *Haematopus ostralegus*, are extreme specialists, feeding on hard-shelled molluscan prey items (see review GOSS-CUSTARD 1996). They increase their intake rate by selecting the most profitable length size of molluscan prey (SUTHERLAND 1982, MEIRE & ERVYNCK 1986, CAYFORD & GOSS-CUSTARD 1990). Within a length class, they select the mussels with the thinnest shells, as this reduces handling time and energy expenditure (DURELL & GOSS-CUSTARD 1984, MEIRE & ERVYNCK 1986, SUTHERLAND & ENS 1987, CAYFORD & GOSS-CUSTARD 1990, NAGARAJAN *et al.* 2002a), in addition, presumably, to reducing the risk of damaging their bill (RUTTEN *et al.* 2006).

The dorsal thickness of mussels declined to its lowest point during December, after which the mussels gradually became thicker and thicker, though still thinner than in autumn. Earlier it was observed in the same study area CAYFORD and GOSS-CUSTARD (1990) that dorsal hammering Oystercatchers started to select

larger mussels starting from December and they selected the largest mussels during February (mean length of 50–55 mm). Although mussels got thicker, the Oystercatchers increasingly took larger mussels which could be associated with shell strength. NAGARAJAN *et al.* (2006) found that the strength of mussels increased after mid-December in the absence of increase in thickness and they speculated that the mussels could bind the calcium more tightly, which could initially increase the strength by changing the microstructures of the shell layers without changing the detectable amount of thickness to respond to predation pressure. LOWELL *et al.* (1994) investigated the shell morphology and strength of marine snails. They found that the strength of *Littorina obthata* (L.) shells increased faster than could be accounted for either overall shell mass or thickness at the point of force application and suggesting that the strengthening could be due to other factors such as changes in the shell microstructure or shape. AKBERALI *et al.* (1983) demonstrated that the *Scrobicularia* mobilised the more tightly bound calcium of the shell during stress conditions which weakened the shell. Clams lost the most recently deposited shell during valve closure at low tides and redeposited the lost shell during the next tidal immersion (AKBERALI *et al.* 1983).

It is well established that Oystercatchers are able to discriminate minute differences between prey items, environment, and even within prey species (GOSS-CUSTARD *et al.* 1995, NAGARAJAN *et al.* 2002a, c). Predators exploit the most profitable prey selectively, which will reduce prey availability across the season (e. g. CAYFORD & GOSS-CUSTARD 1990, SUTHERLAND & ENS 1987, ENS *et al.* 1996). However, the present results show that the mussels get thinner across the winter due to changes in water salinity and temperature. These changes in mussel quality provided important implications as prey on their availability to Oystercatchers. We conclude that the changes in the water quality, especially water salinity and temperature of the aquatic ecosystems, play an important role in determining the characteristics of aquatic life. The top level predators of the food web such as birds are able to track changes in the prey characteristics and adopt a strategy to harvest prey profitably. Thus the prey selection behaviours of these predators can be used as an indicator of the water quality of aquatic habitats.

*

Acknowledgements – R. N. gratefully acknowledges the Leverhulme Trust, London, for funding for this research through an Early Career Award. We are grateful to SÁNDOR ANDRIKOVICS guest editor of *Acta Zoologica Academiae Scientiarum Hungaricae* and BALÁZS ROSIVALL for their valuable comments and suggestions on the paper, PETER GOODES, and DAVE TAYLOR for logistic support, GRAHAM JELFS, REBEKAH BARR, LESLEY CRAIG, and M. E. MAHALAKSHMI for field and lab assistance and Management of AVC College and Government of Tamilnadu for granting leave for R. N. to undertake this research.

REFERENCES

- AKBERALI, H. B., MARRIOTT, K. R. M. & TRUEMAN, E. R. (1977) Calcium utilisation during anaerobiosis induced by osmotic shock in a bivalve mollusc. *Nature* **266**: 852–853.
- AKBERALI, H. B., BREAR, K. & CURRY, J. D. (1983) Mechanical and morphological properties of the shell of *Scrobicularia plana* (Da Costa) under normal and stress conditions. *Journal of Molluscan Studies* **49**: 93–97.
- ALDRIDGE, D. W., PAYNE, B. S. & MILLER, A. C. (1995) Oxygen consumption, nitrogenous excretion, and filtration rates of *Dreissena polymorpha* at acclimation temperatures between 20 and 32 °C. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 1761–1767.
- BOALCH, G. T. (ed.) (1980) *Essays on the Exe estuary*. Exeter. The Devonshire Association, Exeter. 185 pp.
- CAYFORD, J. T. & GOSS-CUSTARD, J. D. (1990) Seasonal changes in the size selection of mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*: An optimality approach. *Animal Behaviour* **40**: 609–624.
- CRENSHAW, M. A. & NEFF, M. J. (1969) Decalcification at the mantle-shell interface in molluscs. *American Zoologist* **9**: 881–885.
- DURELL, S. E. A. LE V DIT. & GOSS-CUSTARD, J. D. (1984) Prey selection within a size-class of mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*. *Animal Behaviour* **32**: 1197–1203.
- DURELL, S. E. A. LE V DIT. & GOSS-CUSTARD, J. D. (1996) Oystercatcher *Haematopus ostralegus* sex ratios on the wintering grounds: the case of the Exe estuary. *Ardea* **84A**: 373–382.
- ENS, B. J., DIRKSEN, S., SMITH, C. J. & BUNSKOEKE, A. J. (1996) Seasonal changes in size selection and intake rate of Oystercatchers *Haematopus ostralegus* feeding on the bivalves *Mytilus edulis* and *Cerastoderma edule*. *Ardea* **84A**: 159–176.
- FECK, J. & HALL, R. O. Jr. (2004) Response of American dippers (*Cinclus mexicanus*) to variation in stream water quality. *Freshwater Biology* **49**: 1123–1137.
- FOX, L. & COE, W. R. (1943) Biology of the Californian Sea mussel: 2. Nutrition, metabolism and growth. *Journal of Experimental Zoology* **93**: 205–249.
- GOSS-CUSTARD, J. D. (ed.) (1996) *The Oystercatchers from individuals to populations*. Oxford University Press, Oxford, 442 pp.
- GOSS-CUSTARD, J. D., CALDOW, R. W. G., CLARKE, R. T., DURELL, S. E. A., LE V DIT & SUTHERLAND, W. J. (1995) Deriving population parameters from individual variations in foraging behavior. 1. Empirical game-theory distribution model of Oystercatchers, *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. *Journal of Animal Ecology* **64**: 265–276.
- GOSS-CUSTARD, J. D., DURELL, S. E. A. LE V DIT., SITTERS, H. P. & SWINFEN, R. (1982) Age-structure and survival of wintering population of Oystercatchers. *Bird Study* **29**: 83–98.
- HARRIS, T. (1980) Invertebrate community structure on, and near, Bull Hill in the Exe estuary. Pp. 135–160. In: BOALCH, G. T. (ed.): *Essays on the Exe Estuary*. The Devonshire Association, Exeter.
- KAUTSKY, N. (1982) Growth and size structure in a Baltic *Mytilus edulis* population. *Marine Biology* **68**: 117–133.
- LOWELL, R. B., FLETCHER, C. R., GRAHME, J. & MILL, P. J. (1994) Ontogeny of shell morphology and shell strength of the marine snails *Littorina obtusata* and *Littorina mariae* – different defence strategies in a pair of sympatric, sibling species. *Journal of Zoology* **234**: 149–164.
- MCGRORTY, S. (1997) Winter growth of mussels *Mytilus edulis* as a possible counter to food depletion by Oystercatchers *Haematopus ostralegus*. *Marine Ecology Progress Series* **153**: 153–165.

- MCGOWAN, A., CRESSWELL, W. & RUXTON, G. D. (2002) The effects of daily weather variation on foraging responsiveness to disturbance in overwintering Red Knot *Calidris canutus*. *Ardea* **90**: 229–237.
- MEIRE, P. M. & ERVYNCK, A. (1986) Are Oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? *Animal Behaviour* **34**: 1427–1435.
- MEZQUITA, F., ROCA, J. R. & WANSARD, G. (1999) Moulting, survival and calcification: the effects of temperature and water chemistry on an ostracod crustacean (*Herpetocypris intermedia*) under experimental conditions. *Archiv für Hydrobiologie* **146**: 219–238.
- MURPHY, S. M., KESSEL, B. & VINING, L. J. (1984) Waterfowl population and limnologic characteristics of Taiga ponds. *Journal of Wildlife Management* **48**: 1156–1163.
- MURRAY, J. W. (1980) The foraminifera of the Exe estuary. Pp. 89–115. *In*: BOALCH, G. T. (ed.): *Essays on the Exe Estuary*. The Devonshire Association, Exeter.
- NAGARAJAN, R., GOSS-CUSTARD, J. D. & LEA, S. E. G. (2002a) Oystercatchers use colour preference to achieve longer term optimality. *Proceedings of Royal Society London B* **269**: 523–528.
- NAGARAJAN, R., LEA, S. E. G. & GOSS-CUSTARD, J. D. (2002b) Re-evaluation patterns of mussels (*Mytilus edulis*) by European Oystercatchers (*Haematopus ostralegus*). *Canadian Journal of Zoology* **80**: 846–853.
- NAGARAJAN, R., LEA, S. E. G., GOSS-CUSTARD, J. D. (2002c) Mussel valve discrimination and strategies used in valve discrimination by Oystercatchers, *Haematopus ostralegus*. *Functional Ecology* **16**: 339–345.
- NAGARAJAN, R., LEA, S. E. G. & GOSS-CUSTARD, J. D. (2006) Seasonal variations in mussel, *Mytilus edulis* L. shell thickness and strength and their ecological implications. *Journal of Experimental Marine Biology and Ecology* **339**: 241–250.
- NAGARAJAN, R. & THIYAGESAN, K. (1996) Waterbirds and substrate quality of the Pichavaram wetlands, southern India. *Ibis* **138**: 710–721.
- NAGARAJAN, R. & THIYAGESAN, K. (1998) Significance of adjacent croplands in attracting waterbirds to the Pichavaram mangrove forests. Pp. 172–181. *In*: DHINSA, G. T., RAO, P. S. & PARASHARYA, B. M. (eds): *Birds in Agricultural Ecosystem*. Society for Applied Ornithology (India), Hyderabad.
- NAGARAJAN, R. & THIYAGESAN, K. (2006) The effects of coastal shrimp farming on birds in Indian mangrove forests and tidal flats. *Acta Zoologica Sinica* **52**: 541–548.
- ODUM, E. P. (1983) *Basic ecology*. Saunders College Publishing, Chicago. 613 pp.
- PATTERSON, J. H. (1976) The role of environmental heterogeneity in the duck populations. *Journal Wildlife Management* **40**: 22–23.
- RAO, K. P. & GOLDBERG, E. D. (1954) Utilization of dissolved calcium by a Pelecypod. *Journal of Cellular and Comparative Physiology* **43**: 283–292.
- RUTTEN, A. L., OOSTERBEEK, K., ENS, B. J. & VERHULST, S. (2006) Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in Oystercatchers. *Behavioural Ecology* **17**: 297–302.
- SANT'ANNA, B. S., ZANGRANDE, C. M., REIGADA, A. L. D. & SEVERINO-RODRIGUES, E. (2006) Spatial distribution and shell utilization in three sympatric hermit crabs at non-consolidated sublittoral of estuarine-bay complex in São Vicente, São Paulo, Brazil. *Revista de Biología Marina y Oceanografía* **41**: 141–146.
- SMITH, P. C. & EVANS, P. R. (1973) Studied of the shorebirds at Landisfarne, Northumberland. I. Feeding ecology and behaviour of the Bar-tailed godwit. *Wildfowl* **24**: 135–139.
- SUTHERLAND, W. J. (1982) Do Oystercatchers select the most profitable cockles? *Animal Behaviour* **30**: 857–861.

- SUTHERLAND, W. J. & ENS, B. J. (1987) The criteria determining the selection of mussels *Mytilus edulis* by Oystercatchers, *Haematopus ostralegus*. *Behaviour* **103**: 187–202.
- WATT, T. A. (1998) *Introductory statistics for biology students*. Chapman & Hall, New York, 236 pp.
- WESTERBOM, M., KILPI, M. & MUSTONEN, O. (2002) Blue mussels, *Mytilus edulis*, at the edge of the range: population structure, growth, and biomass along a salinity gradient in the north-eastern Baltic Sea. *Marine Biology* **140**: 991–999.
- WETZEL, R. G. (1975) *Limnology*. W. B. Saunders & Co, Philadelphia, Pa. 743 pp.

Received July 15, 2007, accepted September 6, 2007, published December 30, 2008