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A year in the life of a Dungeness crab: methodology for determining microhabitat conditions experienced by large decapod crustaceans in estuaries

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Abstract

This study presents a methodology for combining archival data storage tags (DSTs) and ultrasonic transmitters to investigate the microhabitat conditions of adult *Cancer magister* (Dana), inhabiting an estuary. The temperature, salinity and depth experienced by free-ranging Dungeness crabs were recorded at 10-min intervals for periods ranging from 1 week to 8 months. Crabs were tracked using a hydrophone, and tags were recovered via concentrated trapping or returned by recreational fishers for a reward. These methods led to a return rate of 50%. Representative CTD tag data showed that the conditions recorded at fixed stations within the estuary were not reflective of those experienced by free-ranging crabs, but rather crabs were able to orientate and avoid low salinity within the estuary. The prevalence of low salinity exposure was linked to times of increased food availability within the estuary, suggesting that crabs were entering the shallows of the estuary to forage. The techniques used in this study demonstrate that DSTs are a viable means of determining the microhabitat conditions of crustaceans inhabiting highly variable environments.

Introduction

The field of biologging has seen great advancements in recent years as satellite technology and reductions in the size of sensors have made monitoring the habitat conditions experienced by pelagic and benthic marine animals more practical. Multi-sensor tags can record environmental, behavioural and/or physiological data simultaneously, providing key insight into an otherwise unknown realm (Cooke *et al.*, 2004; Block, 2005). While there have been substantial advancements, among marine organisms the majority of these studies have focussed on larger mammals, pelagic fishes and turtles (Hays *et al.*, 2001; Houghton *et al.*, 2002; Block, 2005). Until recently, the large size and exceptionally high cost of the tags used in these studies have prevented the broad scale application of this technology to smaller organisms. However, new techniques are being developed to apply these technologies to smaller organisms (Wilson *et al.*, 2006).

Recent technological advances leading to the miniaturization of commercially available, multi-sensor archival data storage tags (DSTs) have allowed their application in studies involving smaller vertebrates and invertebrates. Through the combined use of telemetric tags for tracking and DSTs, it is now possible to compare the movements of animals within a particular habitat as well as the environmental conditions that they face in 'real time'. Previous studies describing the potential for combining ultrasonic transmitters and DSTs have not explicitly outlined methodology for maximizing returns using these techniques, especially in areas where there is not a commercial fishery for the species in question (Freire & Gonzalez-Gurriaran, 1998; Gonzalez-Gurriaran, Freire & Bernardez, 2002; Wolcott, Wolcott & Hines, 2003).

The influence of environmental conditions such as temperature and salinity on the physiology of decapod crustaceans has been well studied in laboratory conditions (for reviews, see Pequeux, 1995; Whiteley, Taylor & El Haj, 1997; McMahon, 2001). These environmental factors can present significant physiological challenges. A number of studies have examined movements of crustaceans in relation to these environmental conditions based on measurements taken at fixed locations within a particular habitat (Stevens, Armstrong & Hoeman, 1984; Gunderson *et al.*, 1990; Jury, Howell & Watson, 1995; Watson, Vetrovs & Howell, 1999; Bell, Eggleston & Wolcott, 2003; Rewitz *et al.*, 2004), or manual readings taken in the vicinity of tracked or captured animals (Shirley & Wolcott, 1991; Stone & O'Clair, 2001, 2002; Rewitz *et al.*, 2004). However, little is known about the actual scales of exposure to physiologically challenging conditions (Cooke *et al.*, 2004), and the influence that behaviour may have on the duration and severity of exposure (Wolcott & Wolcott, 2001). This is important because the range of conditions used in laboratory studies may not accurately reflect those experienced in the field. For crustaceans inhabiting estuaries, changes in the salinity and temperature regimes within the estuary may have significant effects on their energetics (Guerin & Stickle, 1997; Whiteley *et al*., 2001; Normant & Lamprecht, 2006) and distribution (Barnes, 1967; Watson *et al*., 1999; Rewitz *et al*., 2004).

One such estuarine inhabitant found in the north-east Pacific is the Dungeness crab *Cancer magister*. Despite living in habitats subject to frequent episodes of low salinity, *C. magister* has been classed as a weak osmoregulator (Engelhardt & Dehnel, 1973) and is unable to tolerate salinities below 12‰ (Cleaver, 1949). Because of this relatively low tolerance of hyposaline conditions, alterations in the salinity regime within an estuary can have substantial impacts on the physiology of this species (McGaw & McMahon, 1996; McGaw, 2006) which may affect the crabs' ability to fully exploit hyposaline environments (Barnes, 1967). A number of studies have sought to determine the preferred habitat conditions and distribution of *C. magister* by tracking the movements of crabs fitted with ultrasonic tags (Smith & Jamieson, 1991; Stone & O'Clair, 2001, 2002) or by carrying out trawl surveys and comparing estimates of abundance within an area to the local oceanographic conditions (Stevens *et al*., 1984; Gunderson *et al*., 1990). These studies have provided valuable insights into patterns of estuary use; however, little is known about the microhabitat conditions that individual free-ranging crabs experience.

In this paper, we present a methodology for combining miniaturized DSTs and ultrasonic telemetric tags to monitor the movements of *C. magister* in relation to depth, temperature and salinity. Because *C. magister* can detect differences in salinity as low as 1‰ (Sugarman, Pearson & Woodruff, 1983) and are highly mobile, behavioural adjustments may create different spatial and temporal scales of exposure for free-ranging crabs compared with those observed at fixed stations within the estuary. By using the methodology described here, we were able to record environmental conditions (temperature, depth and salinity) to which individual crabs were exposed in the field. Representative data collected for one individual over an entire year are presented.

Methods

Adult male *C. magister* were trapped in the Sarita River estuary, Barkley sound, British Columbia (49°01.94′N, 125°18.34′W) and transferred to the Bamfield Marine Sciences Centre, where they were held in running seawater (32 ± 1‰; 12 ± 1 °C) for 1 week before release. Crabs were subsequently released in the main river channel of the Sarita River estuary. The Sarita River estuary is located within Numukamis Bay and consists of extensive tidal flats with subtidal eelgrass *Zostera marina* beds at shallower depths. A steep slope towards the seaward side (Fig. 1) extends to a maximum depth of 120 m. Deep water, narrow outlets to the east and west, and a structured, large cobble substrate (circles) likely served to limit emigration from the study area. Crabs were released in July and August 2004, and from July to December 2005.

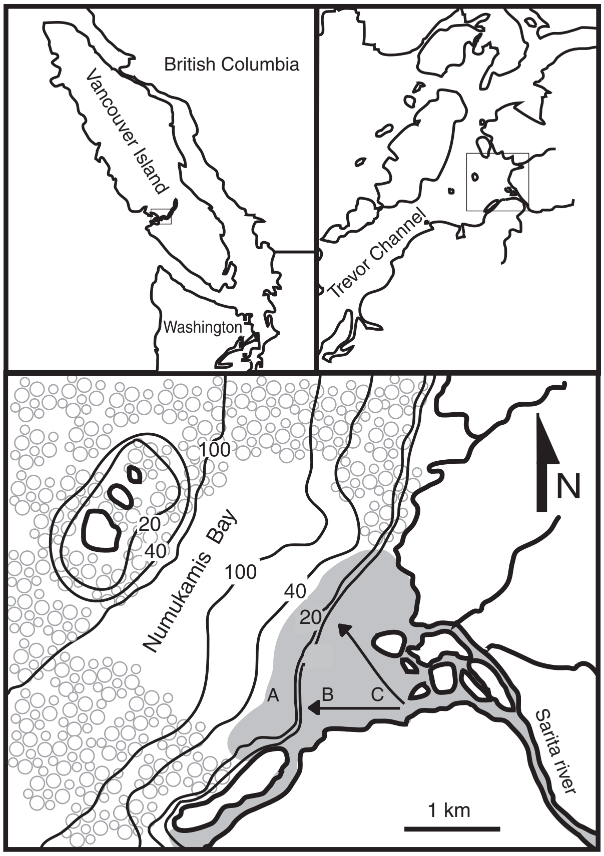

Figure 1 The Sarita River estuary, Barkley Sound British Columbia (49°01.94′N, 125°18.34′W). Circles represent areas of cobble substrate. Grey area represents the influence of freshwater from the Sarita River within Numukamis bay and the two arrows indicate the location and direction of flow in the main channels of the estuary. Letters indicate the 27 m (A), 5 m (B) and 2 m (C) depth fixed stations where temperature, salinity and depth were recorded. Depth contours are in metres below mean low low water.

Previous studies using DSTs to examine the movements and habitat conditions of crustaceans have been restricted to temperature and depth sensors. The DSTs used in this study are unique in that they also incorporate a sensor to measure conductance (salinity). These sensors have only recently (2001) been miniaturized for such applications and have not been widely used for smaller marine organisms (Walker *et al*., 2004; Fukuwaka *et al*., 2005). The temperature, depth and salinity that each crab experienced were recorded in real time using archival DSTs (DST-CTD, Starr-Oddi, Iceland). At a programmed sampling interval of 10 min, the DSTs were able to hold 300 days of data and had a 14-month battery life. Tags weighed 12 g in water and measured 15 × 46 mm. Each tag was inserted into Tygon® tubing (Saint-Gobair Performance Plastics, Arkon, OH, USA) of the same internal diameter as the external diameter of the tag and secured inside the tubing with silicone sealant. This allowed the tag to be easily removed upon capture, and prevented the tag from being damaged. A printed message on the tag could be easily read through the tubing, informing captors of a \$50 reward and providing return instructions. Crabs were also fitted with coded ultrasonic transmitters (CT-82-2E, Sonotronics Inc., Tucson, AZ, USA) that emitted a unique signal for each crab and had a battery life of 14 months. This allowed individuals to be identified and tracked using a directional hydrophone. Ultrasonic transmitters weighed 9 g, measured 54 × 16 mm and were inserted into tubing in the same manner as the DSTs.

Data tags and transmitters were affixed to the dorsal side of the carapace using A788 Splash Zone epoxy (Z-Spar Inc., Los Angeles, CA, USA). Large adult crabs that had recently moulted (identified by shells that had not fully hardened and few epibionts), were used in order to provide the longest possible intermoult period (Wainwright & Armstrong, 1993). The area of the carapace where the epoxy was applied was abraded to maximize adhesion. Moulding the epoxy allowed the tags to be mounted at an upward angle of *c.* 45° immediately posterior to the apex of the carapace (Fig. 2). This means of attachment prevented them from being fouled by mud and sand when crabs buried in the substrate (McGaw, 2005). Once the tags were mounted, crabs were housed in flowing seawater for a period of 24 h, a sufficient time for the epoxy to cure. The entire attachment including both tags and the epoxy weighed <30 g in water and was *c.* 3–4% of the animal's body mass.

Using a directional hydrophone and receiver (Sonotronics DH-4 and USR-96), individual crabs could be located from a small boat at distances up to 1.5 km and their location determined to within 15 m. This allowed crabs to be recovered by focussed trapping efforts. Tagged crabs were also returned by recreational fishermen. Notices advertising the study were posted at local marinas to alert fishermen, and a \$50 reward was offered as an incentive for the return of intact data tags. Once tags were recovered, data were retrieved from the DST using a communication box and Seastar software (Starr-Oddi, Reykjavik, Iceland).

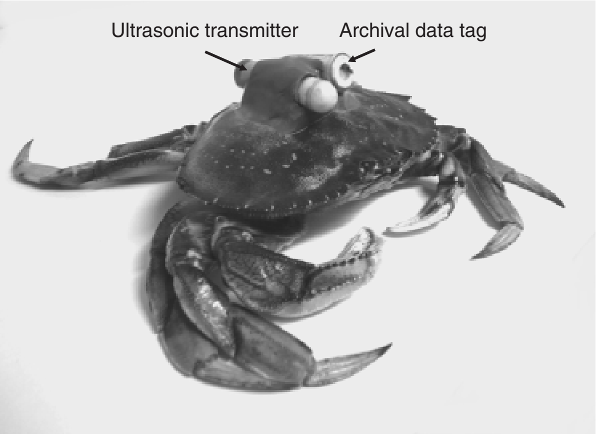

Figure 2 Photograph of an adult *Cancer magister* before its release, fitted with an archival data storage tag and ultrasonic transmitter for tracking. Both tags were held in place on the carapace with moulded Z-spar epoxy.

Processing of data sets (up to 40 000 readings) was accomplished using spreadsheet macros for microclimate data as described by Sinclair (2001). Low salinity exposure was considered to be any exposure lasting >10 min (one sampling interval) at a salinity of <24‰ (75% SW). This salinity was chosen because *C. magister* actively regulate their hemolymph osmolality below this level (Engelhardt & Dehnel, 1973) and exhibit an increase in heart rate (McGaw & McMahon, 1996), which is indicative of a stressful environment (McMahon, 1999).

Oceanographic conditions within the estuary were recorded at three fixed stations during June and October 2005 for a period encompassing a tidal series of spring and neap tides. High discharge rates coupled with a large amount of debris in the estuary prevented recordings during the winter months. The stations were *c.* 300 m apart at depths of 27, 5 and 2 m below mean low low water (MLLW) and were arranged along a transect running east to west in the main river channel (Fig. 1). Station A (27 m depth) was located at the mouth of the estuary where the bottom drops away rapidly, station B (5 m depth) was located within the estuary and station C (2 m depth) was located above station B, further inside the estuary. DSTs were attached to fixed anchors and temperature, salinity and depth were recorded at 10-min intervals. Tags were elevated *c.* 10 cm above the substrate, emulating the conditions that crabs would experience at this location.

Results

Estuary

Decreases in salinity within the Sarita River estuary occurred at regular intervals and corresponded with low tide (Fig. 3). The severity of low salinity within a tide series was inversely proportional to tidal height and varied with season. In June, station A was originally deployed at a depth of *c.* 27 m; however, shortly thereafter the anchor was moved to a depth of about 12 m below MLLW. This is likely the result of an errant fisherman assuming that the float was attached to a trap and not a brick; thus the remainder of readings from the deep station for June were taken at this depth. At the estuary mouth (station A), temperature ranged from a minimum of 10.7 °C to a maximum of 18.6 °C, and salinity ranged from 30.1 to 19.4‰ (Fig. 3a). At station B, temperature ranged between 18.4 and 11.5 °C, and salinity ranged from 31.3 to 20.9‰ (Fig. 3b). Further into the estuary at station C, temperature ranged 18.7–12.7 °C, and salinity ranged 30.4–19.6‰ (Fig. 3c). As the tide receded (depth decreased), the proportion of warm, fresh water in the estuary increased resulting in a decrease in salinity and a concomitant increase in temperature. The magnitude of individual temperature or salinity events was not consistent across stations.

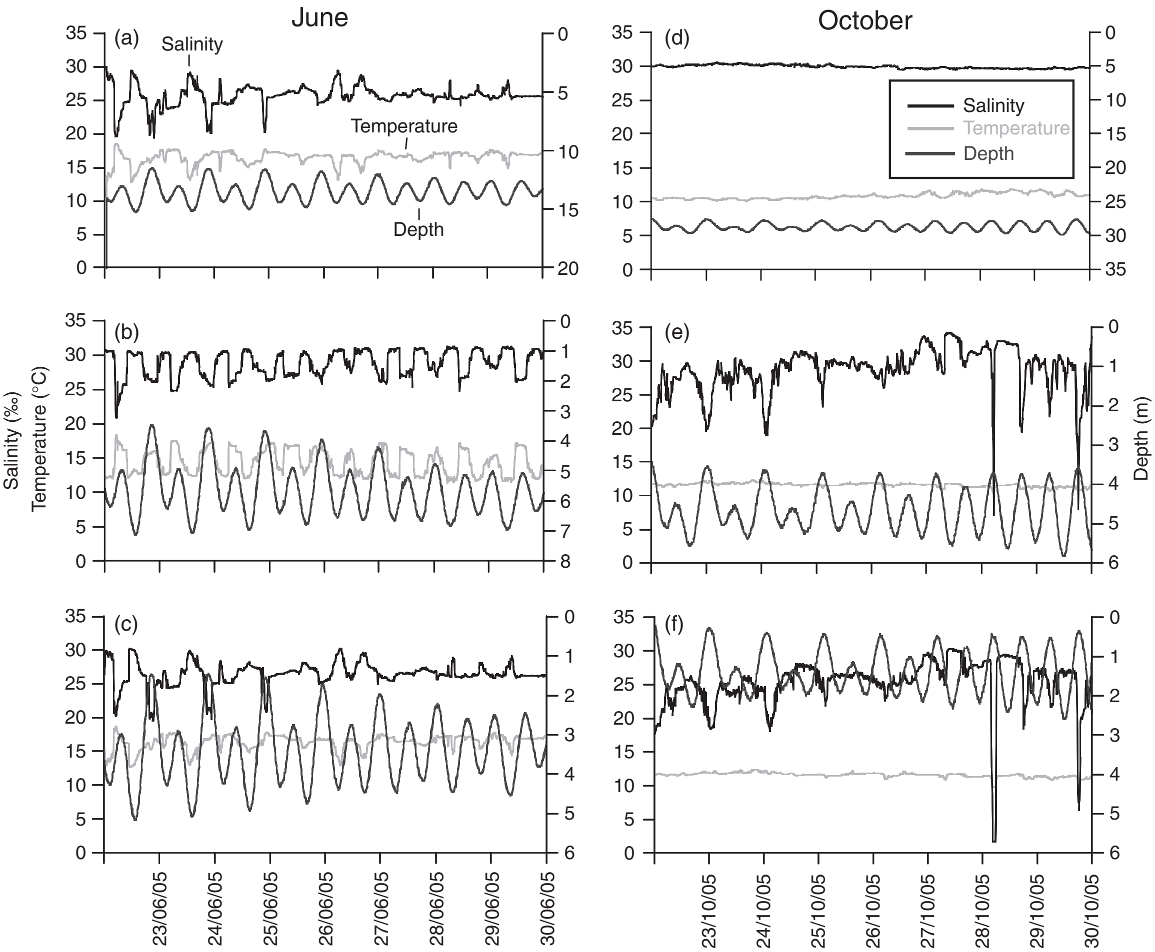

Figure 3 Salinity, temperature and depth recordings measured at 27, 5 and 2 m below mean low low water within the main channel of the Sarita River estuary over a tidal cycle encompassing both spring and neap tides in June (a–c) and October (d–f), 2005.

During the October tidal series, there were only slight changes in temperature, ranging 12.4–9.8 °C; these showed little correspondence to tidal height (Fig. 3d–f). The salinity conditions at the mouth of the estuary (station A), remained constant, ranging between 29.9 and 28.7‰ (Fig. 3d). The changes in salinity further within the estuary at stations B and C were more severe. At station B, salinity ranged between 34.2 and 7.18‰ (Fig. 3e) and at station C, the salinity ranged 30.4–1.7‰ (Fig. 3f). As with the June tidal series, decreases in salinity were associated with low tides. The most severe decreases in salinity corresponded to the largest tidal fluxes.

Tagging

A total of 54 deployments were made, of which 27 tags were recovered, giving a 50% return rate. Of the 27 returns, 70% (19) were returned by recreational fishers in the area, and 30% (8) were recovered by focussing trapping efforts based on tracking data. The length of tag deployment ranged from 5 to 220 days, with a mean deployment time of 44.3 ± 14.8 days and a median deployment time of 16 days. Few tags were recovered between January and April, likely due to inclement weather, which restricted both recreational fishing and directed trapping efforts.

For one individual, Crab A, nearly an entire year of data was collected (Fig. 4a). This individual was first released on 08/30/05. After 90 days at large, the crab was recaptured on 11/29/05 by a recreational fisher. Data from the DST was downloaded and the crab was allowed to recover in the laboratory for 25 days, following which it was re-released in the estuary. This deployment lasted 220 days, and the crab was recaptured on 07/31/06.

Following its initial release directly into the main river channel on 08/30/05, Crab A remained in the shallows of the estuary for 2 days. During this time the crab was exposed to salinity below 75% SW for a total of 40 min, reaching levels as low as 2.2‰ (Fig. 4b). These exposures corresponded with increases in temperature to a maximum of 17.9 °C. Thereafter, the crab retreated into deeper water for a period of 28 days. During this time, the crab remained at depths between 30 and 45 m, with the exception of a few brief

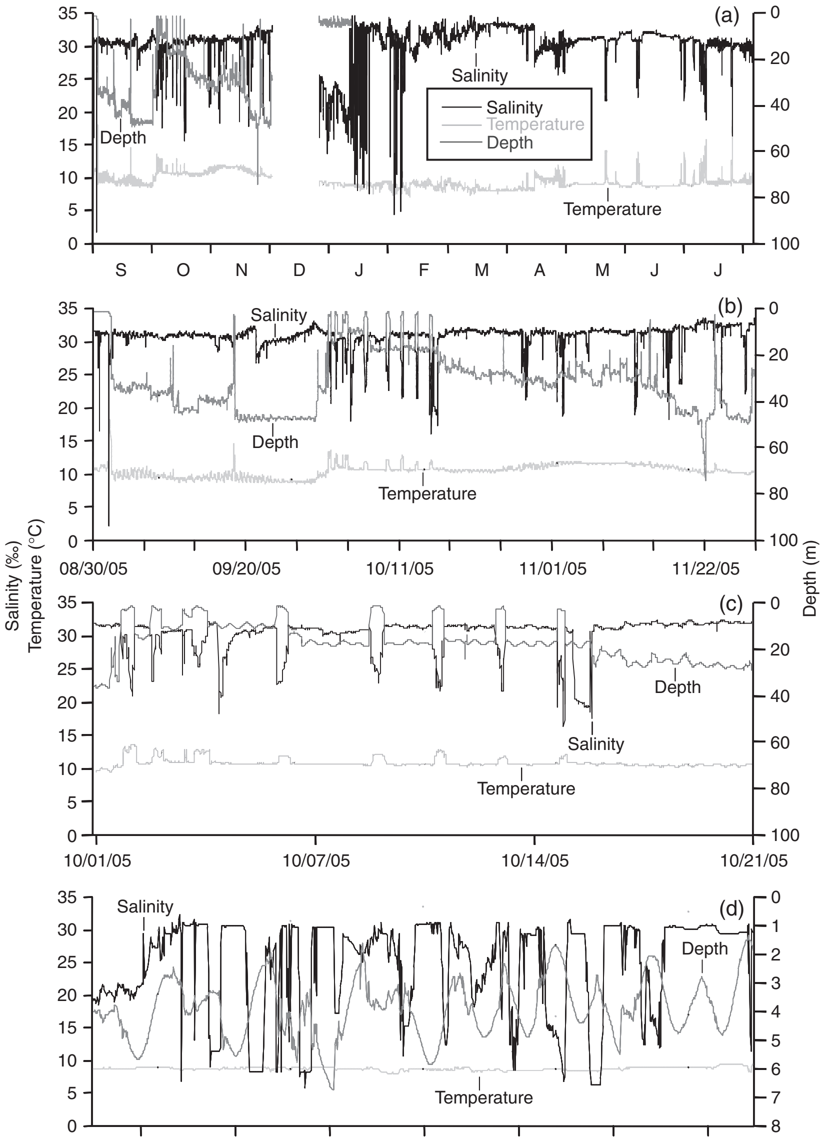

Figure 4 Salinity temperature and depth experienced by Crab A during (a) an entire year, and subsets, (b) first 90 days following release in August 2005, (c) 3 weeks in October, (d) 1 week following re-release in winter.

(< 3 h) forays into water as shallow as 3 m and salinity levels remained above 75% SW. While in deeper water, there were episodes (lasting up to 11 days) during which oscillations in temperature and depth varied with tidal height.

Between 10/01/05 and 10/16/05 Crab A migrated into shallow water (< 24 m) and made a series of eight forays into the littoral zone during nocturnal high tides, each lasting between 6 and 18 h (Fig. 4c). These movements were associated with an increase in temperature from 10.7 up to 13.7 °C and a corresponding decrease in salinity to a minimum of 16.2‰. On 10/16/05, the crab was exposed to salinities ranging from 18.2 to 19.9‰ for a period of 13 h at a depth of 17 m. Following this exposure the crab retreated to depth. Between 10/16/05 and recapture on 11/29/05, the salinity ranges encountered by the crab were highly variable and low salinity exposures of 10 min to 6 h duration occurred at depths of up to 45 m. The temperature remained relatively stable during this time.

Following capture and data upload, Crab A was re-released into the main river channel on 12/23/05, where it remained at depths between 1.5 and 6.6 m for a period of 50 days (Fig. 4d). During this time, the crab was exposed to frequent and severe bouts of low salinity. Exposures ranged from 10 min to 143 h, with a mean exposure time of 4.4 ± 2.5 h. The minimum recorded salinity during this period was 5.2‰. On 02/11/06 the pressure sensor on the DST malfunctioned and no longer recorded accurate depth measurements. From this point until 05/17/06, the crab was not exposed to salinities below 75% SW. However, in mid-April, the crab was exposed to decreased salinities approaching 75% SW and a corresponding increase in temperature for a period of 16 days. From mid-May until

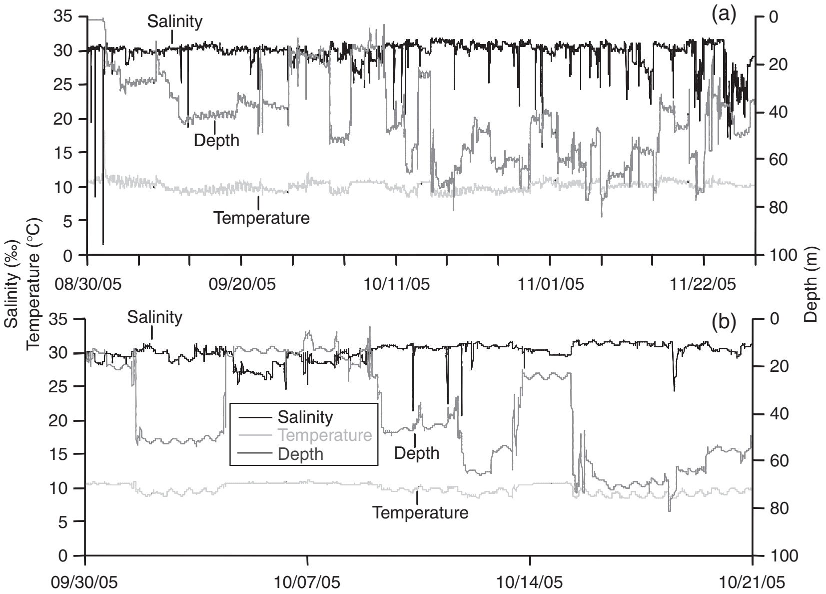

Figure 5 Salinity, temperature and depth experienced by Crab B during (a) 90 days following release in August 2005 and (b) a subset of 3 weeks during October.

its capture in late July, the crab was exposed to short bouts of low salinity below 75% SW along with corresponding increases in temperature. Based on data from other crabs, such exposure to low salinity and increased temperature is indicative of movement into shallower water.

Another crab, Crab B, was also released on 08/30/05 into the main river channel. In the 3 days following release, Crab B was exposed to four episodes of low salinity with the most severe reaching a minimum of 1.6‰ (Fig. 5a). Following this initial low salinity exposure, the crab retreated to depths >20 m and only made two brief forays into shallower water during the next 25 days. Between 09/27/05 and 10/16/05, Crab B made a number of forays into the shallows (<15 m) (Fig. 5b). The timing of this migration corresponded to that observed for Crab A. Coincidentally, Crab B was also recaptured on 11/29/05 by a recreational fisherman; but was never subsequently captured following re-release.

Discussion

A number of articles detail the habitat preferences of decapod crustaceans and the influence of low salinity (Stevens & Armstrong, 1984; Stevens *et al.*, 1984; Gunderson *et al.*, 1990; Smith & Jamieson, 1991; Stone & O'Clair, 2001). However, only a few of these papers report the microhabitat conditions that animals are experiencing in the field (Freire & Gonzalez-Gurriaran, 1998; Gonzalez-Gurriaran *et al.*, 2002; Wolcott *et al.*, 2003). The results of the current study show that the conditions which free-ranging crabs experience are different than those measured at fixed locations within the estuary. For example, during the fall (September–November) Crab A made a series of eight forays into shallow water and these migrations corresponded to nocturnal high tides. This pattern of estuary use by adult *C. magister* also occurs in juveniles (Holsman, McDonald & Armstrong, 2006). Such migrations would provide the least amount of salinity stress due to the correspondence between tidal height and salinity, while minimizing visual predation (Stevens *et al.*, 1984; Gunderson *et al.*, 1990). While previous studies employing trawl sampling during daytime low tides (Stevens & Armstrong, 1984; Gunderson *et al.*, 1990) have provided relative measures of prevalence, these studies may not accurately represent the degree to which adult crabs exploit shallow areas of the estuary. Additionally, trawls do not account for the frequency of individual forays into areas of low salinity. Data presented here suggest that adult crabs migrate in and out of littoral and shallow sublittoral zones with the tide, usually only spending brief periods in low salinity. Patterns of estuary use may therefore not be as clear as is indicated by more infrequent techniques that sample over shorter periods and it is essential that investigators show caution when drawing conclusions about habitat preference without considering the influence of behaviour (Wolcott & Wolcott, 2001).

Methodology

Like many brachyurans, *C. magister* frequently buries itself in the substrate when inactive (Bellwood, 2002; McGaw, 2005). Our preliminary experiments showed that tags mounted parallel to the carapace were fouled with sediment when crabs buried. This resulted in inaccurate salinity measurements due to decreased conductivity across the sensor (D. L. Curtis & I. J. McGaw, unpubl. data). Fouling of the tag was manifested in the data as rapid and severe decreases in salinity. This is easily overcome by comparing the rate of change in the estuary (accounting for locomotory ability) with that observed in the data. In order to reduce the frequency of fouling by sediment when crabs buried, Z-spar epoxy was used to mould the attachment and DSTs were mounted at an upward angle of *c.* 45° relative to the carapace (Fig. 2). The use of a marine epoxy also allowed for the least amount of emersion time for the animal while tags were being affixed because the epoxy cured underwater. Previous studies have used a variety of methods for attaching tags to the carapace of decapod crustaceans, these methods have included 'fast drying' epoxies (Smith & Jamieson, 1991), wiring (Wolcott & Hines, 1990) and even tape (Watson *et al.*, 1999). The combination of Z-spar epoxy and Tygon® tubing used in this study was more effective because it provided a permanent attachment that protected the tags from damage while still allowing them to be easily removed for data transfer.

Adult Dungeness crabs typically moult once per year (Wainwright & Armstrong, 1993). To maximize the length of deployment, recently moulted, adult crabs (>150 mm carapace width), bearing no epibionts were used. This ensured the longest possible intermoult time (Wainwright & Armstrong, 1993), and subsequently the longest possible tag retention. In southern British Columbia and northern Washington, large adult crabs usually moult between late spring and early fall (Orensanz & Gallucci, 1988; D. L. Curtis & I. J. McGaw, unpubl. data). This restriction on the timing of deployments combined with high natural mortality rates likely contributed to the scarcity of recaptured individuals during winter and spring (Smith & Jamieson, 1991). The low median deployment time is likely the result of increased recreational fishing pressure during the summer months. Delaying the release times may have alleviated this, but would also reduce the potential time at large. In support of this, the majority of returns were in the summer; however, most of the longer deployments came from crabs that were released in the late summer.

Ultrasonic signals could typically be detected at distances >1.5 km, and individual crabs could be located to within 15 m under ideal conditions. Nevertheless, the distance at which crabs could be located was restricted during inclement weather, likely due to changes in the signal to noise ratio caused by turbulence in the water (Baras & Lagardere, 1995). While the bathymetry of the site likely limited emigration, it also made the recovery of tagged individuals by SCUBA following death or ecdysis difficult. In a shallower system where recovery by SCUBA is feasible, return rates may be further increased.

Most studies involving the tagging of crustaceans (mark–recapture and DSTs), have relied on intensive commercial fisheries to bolster return rates. Despite this intense effort, the average return rate for these studies is *c.* 23% (e.g. see: Cronin, 1949; Smith & Jamieson, 1991; Fitz & Wiegert, 1992; Watson *et al.*, 1999; Smith *et al.*, 2001; Gonzalez-Gurriaran *et al.*, 2002; Bell *et al.*, 2003; Turner *et al.*, 2003; Wolcott *et al.*, 2003; Aguilar *et al.*, 2005; Yamada *et al.*, 2005). Studies using DSTs to monitor the habitat preferences of decapod crustaceans are rare, likely due to the cost associated with this technology and the low return rates of other tagging studies (Cooke *et al.*, 2004). DSTs and transmitters have been used to measure the depth and temperature experienced by *Maja squinado* as they make seasonal migrations (Freire & Gonzalez-Gurriaran, 1998; Gonzalez-Gurriaran *et al.*, 2002). These studies garnered high return rates (up to 68%), but also relied on an intense commercial fishery for returns. The current study is unique in that it incorporates a salinity sensor and a much finer sampling interval to examine the conditions experienced by crabs in a highly variable habitat. The use of ultrasonic tracking to locate animals followed by concentrated trapping efforts in the vicinity increased the returns, suggesting that this is a viable means of tag recovery in the absence of a commercial or recreational fishery. Combining a relatively high reward for returned tags with our directed trapping lead to a high return rate of 50%.

During the course of this study a few tagged crabs were reported as being captured, but were never returned for reward. The return rate would have been increased had we acquired these tags. Of the tags returned, the data could not be retrieved from two because the membrane on the front of the tag had been punctured and the tag flooded with seawater. The depth sensor on the tag which recorded the data for Fig. 4 ceased to function and depth data are not available for the latter portion of the deployment; however, the temperature and conductivity sensors continued to function. Only one tag showed evidence of biofouling (by a small bryozoan), and this did not appear to affect the performance of the sensors. While the cost associated with this technology has been reduced in recent years, it is still an impediment to the employment of DSTs on the scales of other mark–recapture techniques. Technological advances leading to the miniaturization of archival data tags have opened up a new realm of investigation for large decapod crustaceans. In the current study, the tags and attachment were about 3–4% of the animal's body weight; however, the overall size and weight of the apparatus may prove cumbersome for juveniles or smaller species. In light of this, depth loggers weighing as little as 1 g in water are now available (CEFAS G5 TDR, CEFAS Technology Ltd, Lowestoft, UK), and there is no doubt that small tags such as this will soon be available with greater sensory capabilities.

Representative data

The Sarita River estuary remained stratified in the summer and fall (Fig. 3). As the tide receded, a lens of freshwater travelled seaward towards the mouth of the estuary. The severity of decreases in salinity was greater in October and corresponded to increased rainfall. The data presented here show that during these times the extent of low salinity was restricted to depths shallower than about 27 m below MLLW. However, between the June and October sampling periods, a portion of freshwater flow from the river switched to another channel and flow through what was the main channel was reduced. Therefore the extent of low salinity in the estuary may be greater than the data suggest.

During the summer months, forays into warmer low salinity water were infrequent (Fig. 4a). This is in accordance with data from other crabs that were at large during the same period in 2004 and 2005 (D. L. Curtis and I. J. McGaw, in prep.). An increase in temperature (up to a maximum of 15 °C) leads to increased metabolic and growth rates in juvenile *C. magister* (Gutermuth & Armstrong, 1989; Kondzela & Shirley, 1993). Above 15 °C, the increased energy expenditure associated with respiration limits growth and reduces survival (Kondzela & Shirley, 1993). Because temperatures in the Sarita River estuary regularly exceeded 15 °C during the summer months (Fig. 3), this may have accounted for the scarcity of forays into shallower water. Alternatively, Stevens *et al.* (1984) have linked the prevalence of *C. magister* in estuaries with prey abundance. In the laboratory, crabs are more likely to enter into physiologically challenging conditions when a food stimulus is present (D. L. Curtis & I. J. McGaw, in prep.), suggesting that the number of forays may be linked to relative food availability. In support of this assumption, both Crab A and Crab B made more frequent and prolonged migrations into shallow water in early October (Figs 4b, 5a). These migrations corresponded to the first instances of spawned out salmon carcasses appearing in the Sarita River estuary which has an annual run of *c.* 150 000 fish (S. Ochman, pers. comm.). It has previously been suggested that *C. magister* may enter into areas of low salinity to forage on salmon carcasses at river mouths (Sugarman *et al.*, 1983), and the data presented here appear to substantiate this claim.

Following re-release in late December 2005, Crab A remained in the shallows of the estuary for 50 days and was exposed to salinities as low as 5.2‰. In January 2006, rainfall was more than double the average for that month (www.climate.weatheroffice.ec.gc.ca), possibly contributing to the severe salinity exposures. *Cancer magister* can remain buried in the sediment for prolonged periods during the winter months. However, the depth ranges experienced by the crab did not mimic the tidal cycle indicating that the crab was mobile rather than simply remaining buried in one place. The crab may have remained in the shallows to forage despite the severity of low salinity exposures (Sugarman *et al.*, 1983). In the laboratory, we have found that *C. magister* feeds less frequently in low salinity; however, as the time since their last meal increases, crabs are more likely to enter into low salinity and feed (Curtis & McGaw, 2005). This contradicts previous reports that adult *C. magister* retreat into more stenohaline areas during times of high run-off (Stevens & Armstrong, 1984; Stone & O'Clair, 2002). Coho salmon finish spawning in late December in the Sarita River (S. Ochman, pers. comm.) and with the increased runoff, a large amount of detritus and potential prey items were washed downstream into the estuary (I. J. McGaw, unpubl. data). This again supports the idea that migrations into the estuary are influenced by an increase in food availability (Stevens *et al.*, 1984).

Despite forays into the estuary throughout the year, adult *C. magister* appear to spend the majority of their time at depth where temperature and salinity conditions are more stable. While the lower temperatures at depth may reduce metabolic rate and subsequently growth, it has been suggested that adult crabs are better physiologically adapted to low temperatures (Gutermuth & Armstrong, 1989). Therefore unless there is a gain, such as increased prey availability in the estuary, it would be beneficial for crabs to remain in stable conditions rather than venturing into more ephemeral areas where they will be challenged by higher temperatures or low salinity.

On several occasions, crabs were subjected to particularly severe low salinity conditions that exceeded their physiological tolerance (Cleaver, 1949). Following these exposures crabs retreated to deeper water. Jury *et al.* (1995) reported similar movements for lobsters in response to a freshet following a hurricane. Similar preference behaviours are observed in the laboratory; *C. magister* can detect haloclines and avoid low salinity conditions (D. L. Curtis & I. J. McGaw, in prep.). However, one must be careful about inferring movements in the field solely based upon laboratory experiments. In the laboratory, sharp gradients existed over small spatial scales; in the field where salinity gradients occur on larger scales such directional orientations may not be possible (Bell *et al.*, 2003). Nevertheless, the results presented here suggest that within the Sarita River estuary, crabs are able to orientate to, and avoid low salinity conditions.

This study has demonstrated a methodology for combining miniaturized multi-sensor DSTs, with ultrasonic transmitters for tracking. This work improves upon previous studies (Freire & Gonzalez-Gurriaran, 1998; Gonzalez-Gurriaran *et al.*, 2002), by examining highly variable habitat conditions at a fine sampling scale in the absence of an intense commercial fishery. DSTs provides a viable alternative to well-developed telemetric methods that have successfully been used to monitor the habitat conditions, physiological and behavioural variables of crabs in estuaries (Hines, 2007). To continuously monitor habitat conditions experienced by crabs using telemetry on estuary wide spatial scales, crabs must be continuously monitored (Wolcott, 1995). If manual monitoring is used, only few animals can be at large at once and the duration of deployment is limited by the persistence of the investigator and available boat time. Conversely, to record data from a larger number of individuals or for longer durations, complex hydrophone arrays must by employed (Giacalone *et al.*, 2006). Telemetric tags are limited in the amount of data that they can transmit (Wolcott, 1995), and the ability to detect the signal may be limited in complex habitats (Giacalone *et al.*, 2006). DSTs, however, are not without faults and the key-limiting factor is the need to recover the tags in order to retrieve the data. This can be overcome by combining telemetric tracking tags with DSTs to improve return rates. Another major limiting factor is the high cost. While telemetric tags fabricated in the laboratory are inexpensive, the hydrophone arrays necessary to carry out a study of similar scale using telemetry are costly.

Despite the relatively high cost of DSTs, the high recapture rates attained in this study make this technique a viable and exciting option for monitoring previously unknown physiological and behavioural variables in the field. While the recordings presented here are among the longest in this study, they are representative of the potential data that can be collected using this methodology. The number of annual records for individual crabs may be increased in future studies by a more intensive tracking and trapping programme, and by altering the timing of releases. Additionally, recapture rates may be further increased by using underwater receivers carried by divers and also by attaching small magnets to the carapace so that the DSTs attached to crabs that moult in deep water may be retrieved from the surface. Methods for integrating and analysing the data produced by DSTs are constantly improving and it seems that the only limitation on variables that can be recorded is the ability of an animal to carry the sensors. Recent studies using DSTs on whale sharks have employed fast Fourier transform techniques to examine the periodicity of diving behaviour and its relationship with diel and tidal rhythms (Graham *et al.*, 2006; Shepard *et al.*, 2006). Use of these techniques to examine the relationship between depth and salinity/temperature exposures may be helpful in determining the extent to which crabs are actively or passively exposed to challenging conditions. The potential for determining correlative relationships between biotic and abiotic factors is unlimited. Monitoring the conditions experienced by crabs living in estuaries allows for the use of ecologically relevant parameters for behavioural and physiological experiments, as well as providing data that will be valuable in modelling the energetics and distribution of adult *C. magister* living in estuaries.

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References

Aguilar, R., Hines, A.H., Wolcott, T.G., Wolcott, D.L., Kramer, M.A. & Lipcius, R.N. (2005). The timing and route of movement and migration of post-copulatory female blue crabs, *Callinectes sapidus* Rathbun, from the upper Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* **319**, 117–128.

Baras, E. & Lagardere, J.P. (1995). Fish telemetry in aquaculture: review and perspectives. *Aquacult. Int.* **3**, 77–102.

Barnes, R.S.K. (1967). The osmotic behaviour of a number of grapsoid crabs with respect to their differential penetration of an estuarine system. *J. Exp. Biol.* **47**, 535–551.

Bell, G.W., Eggleston, D.B. & Wolcott, T.G. (2003). Behavioural responses of free ranging blue crabs to episodic hypoxia. I. Movement. *Mar. Ecol. Prog. Ser.* **259**, 215–225.

Bellwood, O. (2002). The occurrence, mechanics and significance of burying behaviour in crabs (Crustacea: Brachyura). *J. Nat. Hist.* **36**, 1223–1238.

Block, B.A. (2005). Physiological ecology in the 21st century: advancements in biologging science. *Integr. Comp. Biol.* **45**, 305–320.

Cleaver, F.C. (1949). Preliminary results of the coastal crab (*Cancer magister*) investigation. *Dept. Fish. Wash. State Biol. Rept.* **49A**, 47–82.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G. & Butler, P.J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* **19**, 334–343.

Cronin, L.E. (1949). Comparison of methods of tagging blue crab. *Ecology* **30**, 390–394.

Curtis, D.L. & McGaw, I.J. (2005). Feeding and digestion in response to low salinity in the Dungeness crab, *Cancer magister*. *Integr. Comp. Biol.* **45**, 983–983.

Engelhardt, F.R. & Dehnel, P.A. (1973). Ionic regulation in the Pacific edible crab, *Cancer magister* (Dana). *Can. J. Zool.* **51**, 735–743.

Fitz, H.C. & Wiegert, R.G. (1992). Local population dynamics of estuarine blue crabs: abundance, recruitment and loss. *Mar. Ecol. Prog. Ser.* **87**, 23–40.

Freire, J. & Gonzalez-Gurriaran, E. (1998). New approaches to the behavioural ecology of decapod crustaceans using telemetry and electronic tags. *Hydrobiologia* **371/372**, 123–132.

Fukuwaka, M., Urawa, S., Yoshimitsu, S., Davis, N.D. & Walker, R.V. (2005) Recoveries of high-seas tags in Japan in 2004, and tag releases and recoveries of fin clipped salmon from Japanese research vessel surveys in the North Pacific Ocean in the summer of 2005. (NPAFC Doc. 889). Hokkaido National Fisheries Research Institute, Fisheries Research Agency, 116 Katsurakoi, Kushiro 085-0802, 12 pp.

Giacalone, V.M., D'Anna, G., Pipitone, C. & Badalamenti, F. (2006). Movements and residence time of spiny lobsters, *Palinurus elephas* released in a marine protected area: and investigation by ultrasonic telemetry. *J. Mar. Biol. Assoc. UK* **86**, 1001–1006.

Gonzalez-Gurriaran, E., Freire, J. & Bernardez, C. (2002). Migratory patterns of female spider crabs *Maja squinado* detected using electronic tags and telemetry. *J. Crust. Biol.* **22**, 91–97.

Graham, R.T., Roberts, C.M. & Smart, J.C.R. (2006). Diving behaviour of whale sharks in relation to a predictable food pulse. *J. R. Soc. Interface*. **3**, 109–116.

Guerin, J.L. & Stickle, W.B. (1997). Effect of salinity on survival and bioenergetics of juvenile lesser blue crabs, *Callinectes similis*. *Mar. Biol.* **129**, 63–69.

Gunderson, D.R., Armstrong, D.A., Shi, Y.B. & McConnaughey, R.A. (1990). Patterns of estuary used by juvenile English sole (*Parophrys vetulus*) and Dungeness crab (*Cancer magister*). *Estuaries* **13**, 59–71.

Gutermuth, F.B. & Armstrong, D.A. (1989). Temperature-dependant metabolic response of juvenile Dungeness crab *Cancer magister* Dana: ecological implications for estuarine and coastal populations. *J. Exp. Mar. Biol. Ecol.* **126**, 135–144.

Hays, G.C., Åkesson, S., Broderick, A.C., Glen, F., Godley, B.J., Luschi, P., Martin, C., Metcalfe, J.D. & Papi, F. (2001). The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *J. Exp. Mar. Biol. Ecol.* **204**, 4093–4098.

Hines, A.H. (2007). Ecology of juvenile and adult blue crabs. In *The blue crab: Callinectes sapidus*: 565–654. Kennedy, V.S. & Cronin, L.E. (Eds). College Park Maryland: Maryland Seagrant College.

Holsman, K.K., McDonald, P.S. & Armstrong, D.A. (2006). Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Mar. Ecol. Prog. Ser.* **308**, 183–195.

Houghton, J.D.R., Broderick, A.C., Godley, B.J., Metcalfe, J.D. & Hays, G.C. (2002). Diving behaviour during the internesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. *Mar. Ecol. Prog. Ser.* **227**, 63–70.

Jury, S.H., Howell, W.H. & Watson, W.H. III (1995). Lobster movements in response to a hurricane. *Mar. Ecol. Prog. Ser.* **119**, 305–310.

Kondzela, C.M. & Shirley, T.C. (1993). Survival, feeding, and growth of juvenile Dungeness crabs from southeastern Alaska reared at different temperatures. *J. Crust. Biol.* **13**, 25–35.

McGaw, I.J. (2005). Burying behaviour of two sympatric crab species: *Cancer magister* and *Cancer productus*. *Sci. Mar.* **69**, 375–381.

McGaw, I.J. (2006). Prioritization or summation of events? Cardiovascular physiology of postprandial Dungeness crabs in low salinity. *Physiol. Biochem. Zool.* **79**, 169–177.

McGaw, I.J. & McMahon, B.R. (1996). Cardiovascular responses resulting from variation in external salinity in the Dungeness crab, *Cancer magister*. *Physiol. Zool.* **69**, 1384–1401.

McMahon, B.R. (1999). Intrinsic and extrinsic influences on cardiac rhythms in crustaceans. *Comp. Biochem. Phys. A* **124**, 539–547.

McMahon, B.R. (2001). Control of cardiovascular function and its evolution in crustaceans. *J. Exp. Biol.* **204**, 923–932.

Normant, M. & Lamprecht, I. (2006). Does scope for growth change as a result of salinity stress in the amphipod *Gammarus oceanicus*? *J. Exp. Mar. Biol. Ecol.* **334**, 158–163.

Orensanz, J.M. & Gallucci, V.F. (1988). Comparative study of postlarval life-history schedules in four sympatric species of *Cancer* (Decapoda. Brachyura: Cancridae). *J. Crust. Biol.* **8**, 187–220.

Pequeux, A. (1995). Osmotic regulation in crustaceans. *J. Crust. Biol.* **15**, 1–60.

Rewitz, K., Styrishave, B., Depledge, M.H. & Andersen, O. (2004). Spatial and temporal distribution of shore crabs *Carcinus maenas* in a small tidal estuary (Looe estuary, Cornwall, England). *J. Crust. Biol.* **24**, 178–187.

Shepard, E.L.C., Ahmed, M.Z., Southall, E.J., Witt, M.J., Metcalfe, J.D. & Sims, D.W. (2006). Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tag data. *Mar. Ecol. Prog. Ser.* **328**, 205–213.

Shirley, M.A. & Wolcott, T.G. (1991). A telemetric study of microhabitat selection by premolt and molting blue crabs, *Callinecttes sapidus* (Rathbun), within a subestuary of the Pamlico river, North Carolina. *Mar. Behav. Physiol.* **19**, 133–148.

Sinclair, B.J. (2001). Biologically relevant environmental data: macros to make the most of microclimate recordings. *Cryo-Letters* **22**, 125–134.

Smith, B.D. & Jamieson, G.S. (1991). Movement, spatial distribution, and mortality of male and female Dungeness crab *Cancer magister* near Tofino, British Columbia. *Fish B-NOAA, US* **89**, 137–148.

Smith, I.P., Jensen, A.C., Collins, K.J. & Mattey, E.L. (2001). Movement of wild European lobsters *Homarus gammarus* in natural habitat. *Mar. Ecol. Prog. Ser.* **222**, 177–186.

Stevens, B.G. & Armstrong, D.A. (1984). Distribution, abundance and growth of juvenile Dungeness crabs, *Cancer magister*, in Grays Harbour estuary, Washington. *Fish B-NOAA* **82**, 469–483.

Stevens, B.G., Armstrong, D.A. & Hoeman, J.C. (1984). Diel activity of an estuarine population of Dungeness crabs, *Cancer magister*, in relation to feeding and environmental factors. *J. Crust. Biol.* **4**, 390–403.

Stone, R.P. & O'Clair, C.E. (2001). Seasonal movements and distribution of Dungeness crabs *Cancer magister* in a glacial southeastern Alaska estuary. *Mar. Ecol. Prog. Ser.* **214**, 167–176.

Stone, R.P. & O'Clair, C.E. (2002). Behaviour of female Dungeness crabs, *Cancer magister*, in a glacial southeastern Alaska estuary: homing, brooding-site fidelity, seasonal movements, and habitat use. *J. Crust. Biol.* **22**, 481–492.

Sugarman, P.C., Pearson, W.H. & Woodruff, D.L. (1983). Salinity detection and associated behaviour in the Dungeness crab, *Cancer magister*. *Estuaries* **6**, 380–386.

Turner, H.V., Wolcott, D.L., Wolcott, T.G. & Hines, A.H. (2003). Post-mating behavior, intramolt growth, and onset of migration to Chesapeake Bay spawning grounds by adult female blue crabs, *Callinectes sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol.* **295**, 107–130.

Wainwright, T.C. & Armstrong, D.A. (1993). Growth patterns in the Dungeness crab (*Cancer magister* Dana): synthesis of data and comparison of models. *J. Crust. Biol.* **13**, 36–50.

Walker, R.V., Davis, N.D., Myers, K.W., Urawa, S. & Hirasawa, K. (2004) Releases and recoveries of U.S. and NPRB salmonid data storage tags, and recoveries of high seas tags in North America, 2004. (NPAFC Doc. 806) SAFS-UW-0406. School of Aquatic and Fisheries Sciences, University of Washington, Seattle WA. 23 pp.

Watson, W.H. III, Vetrovs, A. & Howell, W.H. (1999). Lobster movements in an estuary. *Mar. Biol.* **134**, 65–75.

Whiteley, N.M., Robertson, R.F., Meagor, J., El Haj, A.J. & Taylor, E.W. (2001). Protein synthesis and specific dynamic action in crustaceans: the effects of temperature. *Comp. Biochem. Physiol. A* **128**, 595–606.

Whiteley, N.M., Taylor, E.W. & El Haj, A.J. (1997). Seasonal and latitudinal adaptation to temperature in crustaceans. *J. Therm. Biol.* **22**, 419–427.

Wilson, R.P., White, C.R., Quintana, F., Halsey, L.G., Liebsch, N., Martin, G.R. & Butler, P.J. (2006). Moving towards acceleration estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* **75**, 1081–1090.

Wolcott, T.G. (1995). New options in physiological and behavioural ecology through multichannel telemetry. *J. Exp. Mar. Biol. Ecol.* **193**, 257–275.

Wolcott, T.G. & Hines, A.H. (1990). Ultrasonic biotelemetry of muscle activity from free-ranging marine animals: a new method for studying foraging activity by blue crabs (*Callinectes sapidus*). *Biol. Bull.* **176**, 50–56.

Wolcott, T.G. & Wolcott, D.L. (2001). Role of behaviour in meeting osmotic challenges. *Am. Zool.* **41**, 795–806.

Wolcott, T.G., Wolcott, D.L. & Hines, A.H. (2003). Exploring migration of female blue crabs to spawning grounds, using biotelemetry and CTD dataloggers. *Integr. Comp. Biol.* **43**, 1001–1001.

Yamada, S.B., Dumbauld, B.R., Kalin, A., Hunt, C.E., Figlar-Barnes, R. & Randall, A. (2005). Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific. *Biol. Invas.* **7**, 309–321.