Hydrobiologia **371/372:** 123–132, 1998.
J.-P. Lagardère, M.-L. Bégout Anras & G. Claireaux (eds), Advances in Invertebrates and Fish Telemetry.

New approaches to the behavioural ecology of decapod crustaceans

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Key words: behavioural ecology, crustaceans, decapods, electronic tags, migrations, telemetry

Abstract

Decapod crustaceans have complex life histories and behaviour in aspects such as foraging, mating and reproduction, moulting and growth, habitat selection and migration. New technologies have enabled us to use an individual, field-based approach to analyze these problems, although they have been less developed in decapods than in marine vertebrates. These new possibilities are discussed here mainly from a biological point of view. There is a brief review of previous applications of telemetry to analyze habitat selection, foraging behaviour, energetics, moulting site selection and migrations in decapods, and two case studies are discussed in more detail. The first one refers to the study of differences in habitat use and movement patterns in juveniles and adults of coastal species that show ontogenetic habitat shifts, related to differences in selective pressures affecting both life history stages (predation risk, and growth and reproduction optimization). The second case study is dedicated to the migratory patterns in spider crabs combining telemetry and electronic tags. Operational limitations in tracking make it impossible to get detailed information on movement patterns during migration, which in turn involve an important bathymetric gradient and a change in the oceanographic environment (mainly temperature). Monitoring depth and temperature in the immediate habitat of the animals, using electronic data storage tags recovered by the fishery, allow for movement patterns to be modeled using supplementary information on the topography and hydrography of the study area. This approach is being tested using both telemetry and electronic tags simultaneously.

Introduction

The application of telemetry techniques to marine organisms has made it possible to track and determine their location on a continuous and individual basis in the field (Stasko & Pincock, 1978; Hawkins & Urquhart, 1983; Priede & Swift, 1992; Urquhart & Stewart, 1993) as well as to monitor physiological and behavioural parameters (O'Dor et al., 1988; Butler, 1989; Wolcott & Hines, 1989a; Kasello et al., 1992). With this information on an individual level, it is possible to analyze the relationship between physiological and behavioural changes and the environmental factors which determine them. Decapod crustaceans have complex life histories and behaviour in aspects such as foraging, mating and reproduction, moulting and growth, habitat selection and migration. Some of these biological characteristics make these marine invertebrates, along with the cephalopods, appropriate for the application of telemetry following the techniques designed for fishes or specific new methods. Since many decapod species have a large body size and high mobility, and they occupy easily accessible benthic and coastal habitats, it is possible to track them telemetrically.

Decapod crustaceans have certain peculiarities in their life histories which should be taken into consideration when establishing the methodology of study. The discontinuous growth through moults brings about the loss of the exoskeleton and consequently of external tags, although some species do undergo a terminal moult. However the presence of an exoskeleton offers some advantages for attaching external tags and

Table 1. Studies on the behavioural ecology of marine decapod crustaceans that have used biotelemetry techniques

Species	Author	Tracking system	Carrier	Telemetered variables	Behaviour	Observations
BRACHYURAN CRABS						
CANCRIDS						
Cancer magister	Smith & Jamieson (1991)	D	U	Location	Movement, Dispersal	
Cancer pagurus	Bottoms & Marlow (1979)	–	U	Heart rate		Laboratory testing
	Hall et al. (1991)	AC	U	Location	Movement	Sediment disturbance
	Skaaja et al. (1998)	AC	U	Location	Movement	
PORTUNIDS						
Callinectes sapidus	Wolcott & Hines (1990), Shirley & Wolcott (1991)	D	U	Location, Ecdysis	Habitat use	
	Wolcott & Hines (1989a, b), Nye (1989)	C	U	Location, Madibular muscle activity	Foraging	
	Clark, Hines & Wolcott (pers. comm.), Wolcott (1995)	AC,C	U	Location, Mandibular muscle activity, Cheliped display	Foraging, Agonistic behaviour	
	Hines et al. (1995), Hines, Wolcott, Freire & Ruiz (unpubl. data)	D	U	Location	Movement, Habitat use	
Scylla serrata	Hill (1978)	C	U	Location	Movement	
MAJIDS						
Chionoecetes opilio	Maynard & Webber (1987), Maynard (1991)	AC,D	U	Location, Branchial pressure	Movement, Energetics, Habitat use	Energetics in laboratory
Maja squinado	González-Gurriarán & Freire (1994), Hines et al. (1995)	D	U	Location, Temperature	Movement, Migration, Habitat use	
OCYPODIDS						
Ocypode quadrata	Wolcott (1980a, b)	D	R	Location, Heart rate, Temperature	Movement, Energetics, Habitat use	Intertidal
ANOMURAN CRABS						
Paralithodes camtschaticus	Monan & Thorne (1973), Stone et al. (1992, 1993)	D	U	Location	Movement, Migration, Habitat use	
LOBSTERS						
Homarus americanus	O'Dor & Webber (1991)	AC	U	Location, Temperature	Movement	
Homarus gammarus	Collins & Jensen (1992)	D	U	Location	Movement	
	Collins et al. (1993), Smith et al. (1998)	AC	E	Location	Movement, Habitat use	
Nephrops norvegicus	Chapman et al. (1975)	AC	U	Location	Movement	
	Bjordal et al. (1993)	AC	U	Location	Movement	
Panulirus cygnus	Phillips et al. (1984), Jernakoff (1987a, b), Jernakoff et al. (1987)	AC	E	Location	Movement, Habitat use	

Tracking system: D, discontinuous, C, continuous (non automated); AC: automated continuous (stationary array of omnidirectional hydrophones or aerials)
Carrier: U, ultrasonic; R, radio; E, electromagnetic
Telemetered variables: environmental variables (temperature) are only included if they were measured using telemetry (variables measured using other systems after positioning are not included)
Behaviour: Movement, includes speed and distance of displacements, orientation and timing. Habitat use, characterization of the habitat used in relation to its environmental characteristics (depth, temperature, salinity, vegetation)

locating internal structures. Decapods are mobile organisms and the large-sized walking species show major differences in the energetic costs of movement respect to swimming fishes. Although, as a rule, the range of movements in decapods is smaller than in fishes (see references cited in Table 1), some species cover large distances during migration.

Methods for the study of behaviour in decapod crustaceans

The primary source of information on the behaviour of decapods comes from laboratory studies which entail certain limitations, particularly in large-sized species, and they do not allow for an analysis of certain aspects such as migrations. Urquhart & Stewart (1993) have reviewed the methods for the field observation of the behaviour of fishes which are basically the same as those used on decapods.

Direct observation by divers or video provides information on habitat use, movements and biotic interactions (e.g. Karnofsky et al., 1989 a,b), but it is not possible to record the physiological activity and this type of observations are restricted to shallow waters with adequate light (diving) and/or small areas (both methods).

The mark-recapture experiments (see review by Emery & Wydoski, 1987) have used magnetic tags (Hurley et al., 1990) or biological tags (Shelton & Chapman, 1987) involving internal implantation, or external tags (for example T-bar tags, Hurley et al., 1990). In all cases tagging presents different problems related to handling the animal, mortality induced, or tag shedding. Despite these limitations, the mark-recapture experiments have provided data of great interest on population dynamics and large scale migration patterns in crustaceans. However, from a behavioural point of view, their application is limited since only sporadic data on the location and biological state of the tagged animals can be recorded. Moreover, the fact that the animal must be recovered means that these methods apply mostly to commercial species where the fishing effort allows an acceptable recapture rate.

As an alternative to these tags, which we may call conventional, systems have been developed based on passive integrated transponders (PIT tags), which, because of their small size, make it possible to study juvenile individuals or small-sized species (Van Montfrans et al., 1986, 1991; Fitz & Wiegert, 1991). Despite the progress made with this new system, the problem of recapture persists. In this case, given the technical characteristics of this system, the samplings are generally realized for this purpose, which makes it possible to apply an experimental design, more appropriate than the commercial fisheries, however the size of the study area is limited.

Telemetry is a step forward in the study of behaviour in the field as compared to the methods discussed earlier. Ultrasonic telemetry techniques have led to detailed studies of the behaviour and energetics of marine organisms in the field (O'Dor et al., 1988, 1993, 1994; Butler, 1989; Wolcott & Hines, 1989b, 1990; Shirley & Wolcott, 1991; Kasello et al., 1992). The technological advancements in the construction of ultrasonic transmitters have led to the use of much smaller components and an increase in battery life, making it possible to apply them to invertebrates such as decapod crustaceans (see below) or cephalopods (e.g. O'Dor et al., 1993, 1994).

The recent introduction of electronic data storage tags or archival tags, allows for the continuous monitoring of the immediate environment, the microenvironment, of the animal, although they do not eliminate the necessity for recapture. To date the use of these tags has been much more restricted than the application of telemetry, not counting the great number of studies done on marine mammals and birds, but they have begun to provide important information on the migration of several species of fish (Metcalfe et al., 1994; Gunn et al., 1994, Sturlaugsson, 1995; Thorsteinsson, 1995).

A brief review of the application of telemetry in the study of the behavioural ecology of decapod crustaceans

Table 1 presents a review of the studies that have applied telemetry techniques to marine crabs and lobsters. The most commonly used systems have been the ultrasonic ones, except in specific cases such as in intertidal areas or structurally complex habitats (e.g. reefs) where, on occasion, radiotelemetry or electromagnetic systems have been used respectively. Wolcott (1995) has recently reviewed the application of telemetry techniques in the study of behavioural and physiological ecology of decapod crustaceans. This author analyzes the different options currently available, mainly from a technological standpoint. The conclusions we may draw from this review are that with the technology currently available it is possible to record information on virtually any variable related to the behaviour, physiology and microenvironment of these animals.

Despite the wealth of potential applications of telemetry, most of these studies have consisted only of tracking the animals tagged with pingers in order to get information on their patterns of movement, dispersal and migrations, and habitat use. In most cases the characteristics of the environment occupied by the tagged individuals have been recorded by means of samplings coinciding with the positioning of their location without the use of telemetry (with some exceptions as is the case of temperature). Although these types of studies have not developed the full range of potential that telemetry has to offer, in terms of internal and microenvironmental variables, they have implemented automated systems of continuous tracking which have provided detailed information on the movements of the tagged individuals in space and time.

However, the use of telemetry of physiological and behavioural parameters in the field has not gained widespread use in decapods. Despite the early experiments and calibrations carried out in the laboratory as far back as the 1970's (Bottoms & Marlow, 1979), only Wolcott (1980a, b) working with *Ocypode quadrata* and Wolcott, Hines and collaborators (see references in Table 1 and a brief description in Wolcott, 1995) with *Callinectes sapidus* have performed experiments in the field in which the energetic costs or different aspects of foraging and agonistic behaviour have been measured. Thus the wide range of telemetry systems presented by Wolcott (1995) as technologically feasible at the present time remain largely unexplored in terms of their potential application in the field.

Two case studies of the use of telemetry and electronic tags in decapod crustaceans

This Section provides a more in-depth look at two examples of the application of telemetry and related techniques, such as the use of electronic data storage tags, for the study of the behavioural ecology of crustaceans. These case studies aim to illustrate the wide potential of telemetry, even with the simplest applications, for testing in the field different hypotheses on behavioural mechanisms and life histories of decapods. The application of new technologies available that will help overcome some of the limitations inherent to telemetry is discussed.

Habitat utilization and movement patterns in juvenile and adult crabs

The results presented by several authors on different coastal species of crabs and lobsters (see Hines et al., 1995), using research techniques such as field samplings, mark-recapture or laboratory experiments have, in most cases, pointed to the existence of differences in the characteristics and range of movements and habitat selection between juveniles and adults, often involving migrations (directional long-distance movements that entail drastic changes in habitat) after the pubertal moult.

González-Gurriarán & Freire (1994), Hines et al. (1995) and Hines, Wolcott, Freire & Ruiz (unpublished data) analyzed ontogenetic changes (between juveniles approaching maturity and adults) in two species of crabs with great differences in their life histories and habitat (the coastal spider crab *Maja squinado* and the estuarine blue crab *Callinectes sapidus*, in the NE and NW Atlantic respectively). The two studies are an example of simple telemetry applications in behavioural ecology, using discontinuous tracking to estimate the variables of movement (speed, distance and orientation) and habitat use (depth, bottom type)

Maja and *Callinectes* have patterns of behaviour and habitat utilization similar to those described in other species. The telemetry experiments show the immediate behavioural mechanisms that determine these patterns, making it possible to obtain individualized information on free-ranging animals (Table 2). In both species, juveniles present restricted (in areas < 500 m), non-directional movements in shallow, structurally complex habitats (rocky kelp beds or soft bottoms with wood debris). On the other hand adults have broader ranges of movement with a strong directionality (in zones > 1 km and far greater distances during migration, at much faster speeds than the juveniles) in the deeper areas (up to over 100 m in *Maja*), where they use, to a greater extent, less complex soft bottoms. In *Maja*, once adults reach sexual maturity after the terminal pubertal moult, they exhibit two clearly differentiated phases in their movements and habitat (Table 2). In the first phase, prior to migration, their behaviour is similar to that of juveniles, although both depth and speed increase slightly. The second phase, which corresponds to beginning of the

Table 2. Movements patterns of juvenile and adult crabs tracked with ultrasonic telemetry. Experiments on *Maja squinado* were carried out in the Ría de Arousa (Galicia, NW Spain) from summer 1993 to winter 1994, and on *Callinectes sapidus* in the Rhode River (a subestuary of Chesapeake Bay, USA) in summer 1993. For each parameter, mean and standard error (in parentheses) are shown. Positioning was carried out with respect to landmarks and buoys (juveniles) or using GPS (adults) for *Maja* and using landmarks for *Callinectes*. Body size was measured as carapace length in *Maja* and carapace width in *Callinectes*. The orientation was measured using the statistic r which represents the directionality of the different displacements (between successive locations) of each individual (0: random orientation, 1: all displacements with the same bearing). See González-Gurriarán & Freire (1994) and Hines et al. (1995) for more details

	Maja squinado			*Callinectes sapidus*	
		Adults			
	Juveniles	Pre-migration	Start of migration	Juveniles	Adults
Number of crabs	8	5	6	12	8
Body size (mm)	107.0 (5.6)	145.0 (5.9)	150.0 (6.6)	100.2 (2.3)	148.5 (3.2)
Tracking time (days)	43.5 (6.1)	52.9 (28.8)	27.6 (5.5)	12.8 (0.8)	10.2 (1.9)
Speed (m day^{-1})	6.5 (1.2)	22.1 (6.1)	75.8 (16.2)	156.7 (22.3)	328.1 (43.9)
Depth (m)	4.5 (0.7)	7.3 (0.8)	14.0 (2.5)	1.3 (0.1)	2.6 (0.2)
Orientation (r)	0.14 (0.03)	0.35 (0.11)	0.81 (0.05)	0.32 (0.05)	0.61 (0.08)

migration, is characterized by directional movements towards deeper zones at a greater speed.

These findings have led to a number of hypotheses on the adaptive value of the ontogenetic changes in behaviour and habitat utilization, which are based on the type of selective pressures affecting juveniles and adults, and which would be similar in the different decapods living in the coastal areas. Predator avoidance and growth optimization are the selective forces of the behavioural patterns observed in juveniles. The maximization of reproductive success, through a successful incubation process, largely dependent upon temperature and salinity, and the release of larvae in habitats adequate to survival, determines adult behaviour and brings about the postpubertal migrations. The results from the use of telemetry have made it possible to characterize the habitat and movements of juveniles and adults, and therefore, lay the foundations for future studies that will allow the proposed hypotheses to be tested. For example, Hines & Ruiz (1995) show that the nearshore shallows constitute a refuge for the juveniles of*Callinectes* against cannibalism.

Migrations in spider crabs

Telemetry has a number of drawbacks stemming from the difficulty in the continuous tracking of animals at sea. In fact, in the case of the spider crab *Maja squinado*, these operational problems prevent the detailed tracking in the phase where the animals migrate to deep off-shore waters (González-Gurriarán & Freire, 1994).

In species where the recapture of tagged individuals is feasible, mainly due to the fact that they are exploited by fisheries, alternative (non-telemetry) techniques have been used which involve the attachment of electronic tags to store data on the microenvironment or physiological or behavioural variables of the animal. These data can be downloaded after recapture takes place. The miniaturization of these tags has allowed them to be used in the study of fish migrations (Metcalfe et al., 1994; Gunn et al., 1994, Sturlaugsson, 1995; Thorsteinsson, 1995).

This application of this methodology is based on the fact that during their migrations the tagged animals move across important environmental gradients, some of which are used as an orientation mechanism. The continuous monitoring of the environmental parameters involved (such as depth, temperature, salinity or light) along with the baseline data on habitat characteristics (topography, oceanography) make it possible to reconstruct the tracks of the animals, estimating the temporality, directionality, and movements carried out throughout the migration. Arnold & Holford (1995) have presented a simulation model based on tidal streams, which when linked to previous knowledge on behaviour will enable us to reconstruct the movements of different fish species from temperature and depth data assimilated continuously by electronic tags.

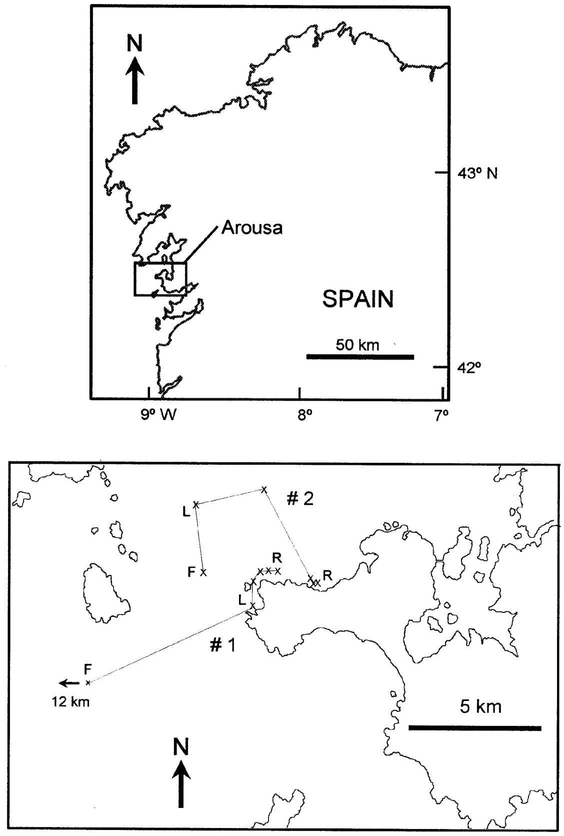

Figure 1. Migrations of the spider crab *Maja squinado* in the Ría de Arousa and adjacent coastal area (Galicia NW Spain) using telemetry and electronic data storage tags. The tracks of two adult females, tracked approximately at weekly intervals using telemetry in 1997, are shown (release point R, last telemetered location L and point of recapture by the commercial fishery F are shown).

Based on the hypothesis that the migrations of the spider crab *Maja* involve important bathymetric changes and movements between water masses having distinct oceanographic characteristics (temperature and, to a lesser extent, salinity), a experiment have been started for the purpose of calibration and use of electronic tags as a tool to study migrations. Moreover, earlier data point to a high fishing mortality rate (tangle-nets and glass-box gears) on the SW coast of Galicia (NW Spain). Previous telemetry experiments had over 70% recapture rates. However, *Maja* undergoes a terminal moult, which means that adults, which is the life stage involved in the migrations do not have additional ecdyses (González-Gurriarán et al., 1995) and that they may be tagged with devices attached to the carapace.

In the summer of 1996 an experiment was begun in the outer area of the Ría de Arousa (Figure 1) in order to compare the behavioural patterns of primiparous and multiparous adult females (in their first annual reproductive cycle or consecutive cycles, respectively; see González-Gurriarán et al., 1993, 1998) by means of a combination of telemetry and electronic tags. Each individual was tagged with an ultrasonic transmitter (V16 of VEMCO, Canada and CHP-87-S-M of SONOTRONICS, United States) and an electronic tag for temperature and depth (DST-100 of STAR ODDI, Iceland and MINILOG-TDX of VEMCO), which comprised $< 5\%$ of the body weight. We carried out tracking discontinuously, at intervals of approximately 1 week, in order to locate the animals with telemetry.

Our results to date have shown a recapture rate $> 60\%$ (11 recaptures from 18 releases of tagged females). The information provided by the electronic tags point to autumn migrations defined by important bathymetric changes during short periods of time (Figure 2). During this migration, females moved from an average depth of 12 m (range: 7–17 m) to 63 m (range: 36–96 m). The mean duration of these movements to deep waters was of 10 days (range 4–16 days) and occurred in early November (mean dates of start and end of migratory movements: 7 and 16 November), although extended from September to January for the different crabs. During these movements the tagged animals travel through clearly differentiated thermal environments characterized by different substrate types. The available data on bathymetry in the study area and its oceanography (based on a network of oceanographic stations sampled weekly and continuous records of temperature in the shallow areas where the animals were released) allow us to reconstruct the tracks of the tagged individuals. These estimates may be analyzed in relation to the positionings provided by telemetry. The preliminary analyses of the available data suggest that these two methods of estimating migration routes are basically in agreement. Moreover, this information enables us to define the behavioural rules that animals follow to orient themselves throughout the migration, based primarily on the depth gradient. This migration is characterized by a shift towards the deeper zones in autumn, when the temperature and salinity in the shallow waters drop, and a return to these areas at the end of winter and spring, which coincides with the incubation period.

These preliminary results point to the possibility of reconstructing the tracks of animals equipped with

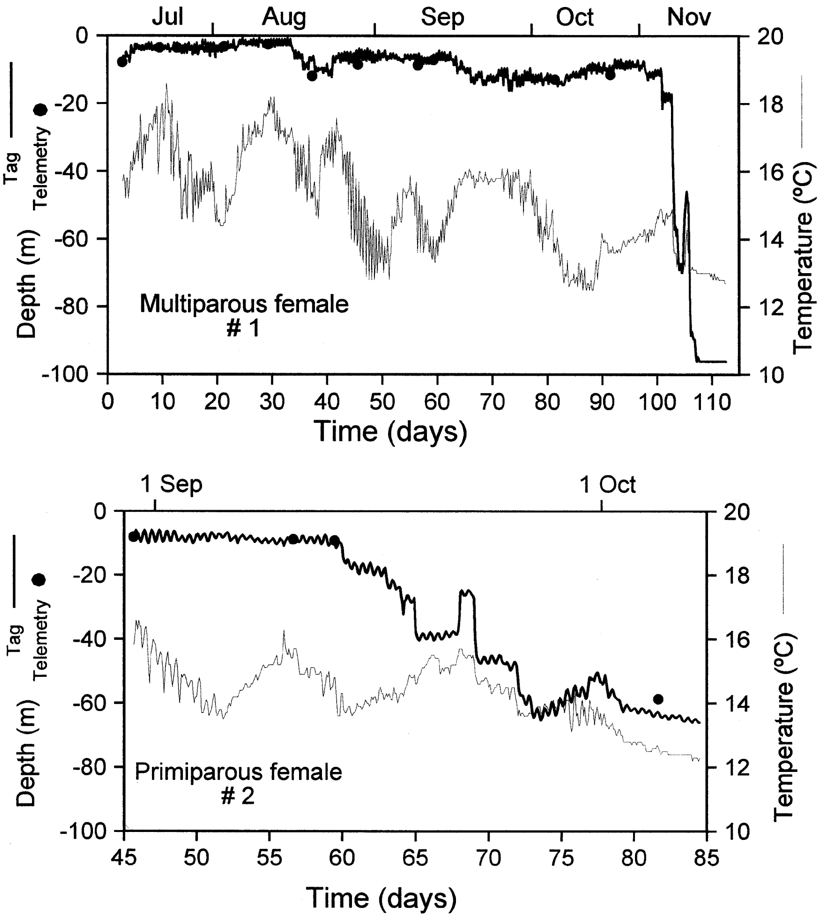

Figure 2. Migrations of the spider crab *Maja squinado* in the Ría de Arousa and adjacent coastal area (Galicia NW Spain) using telemetry and electronic data storage tags. Temporal evolution of the habitat depth and temperature of two females measured every two hours by means of eletronic tags and the depth at which they were located using telemetry. Depth was not corrected by the effect of the tide (maximum variation of aprox. ±3 m). The data series of the electronic tags covers the period from the release of the females to their recapture by the commercial fishery (day 0 = 15 July 1996). The tracks of both females obtained by telemetry are showed in Figure 1.

electronic tags based on information from their microenvironment provided by these devices and on the understanding of their orientation mechanisms. The second part of the experiment will attempt the large-scale use of electronic tags in order to determine the spatial variability (between nursery grounds) and between males and females in migration characteristics.

Future directions in the telemetry of decapods and alternative methods

The future development of telemetry and related techniques in the study of the behavioural ecology of decapod crustaceans appears to be feasible using the technology currently available. Three broad areas of interest may be defined in which the technology which is currently available or soon to be developed, can help to provide a more in-depth knowledge of the biological problems posed by the decapods.

The automated systems of ultrasonic telemetric tracking have already been used both in fishes (Urquhart & Smith, 1992; Bjordal et al., 1993) as well as in invertebrates (Maynard & Webber, 1987; O'Dor et al., 1988; Wolcott, 1995). The use of these telemetric systems for physiological and behavioural parameters would provide detailed information on the temporal and spatial patterns of individual behaviour and on biotic interactions (mating, foraging and social behaviour) and with the physical environment (O'Dor et al., 1988; Wolcott, 1995). These systems may be applied to animals that carry out their activity in restricted areas. However, with animals that move over great distances, telemetry has its limitations due to the fact that it depends on direct work in the sea. The current problem with electronic tags is the recapture of the tagged animal and the bias created by the spatial distribution of the fishing effort. The development of recovery systems, whether they involve the tag (which may fall off the animal at any time, and emitting a signal that will allow it to be recovered) or information (through interrogation at permanent stations and activation of an ultrasonic system for transmitting information) will enable us to solve the problems facing us at the present time.

The telemetry of physiological parameters (Butler, 1989) has revolutionized our understanding of bioenergetics in fishes (Lucas et al., 1993; Claireaux et al., 1995a, b) and cephalopods (O'Dor et al., 1993, 1994). The applications developed for crustaceans are presently restricted to the calibration in the laboratory of the relationship between the recorded variable and energy consumption (Maynard, 1991), and to studies in the field that relate foraging to muscular activity (Nye, 1989; Wolcott & Hines, 1989a, b; Wolcott, 1995). Nowadays it is possible to monitor different physiological processes (such as heart rate and respiratory activity by recording biopotentials or pressure variations in the branchial chamber), which are closely linked to energy consumption. Thus, in the near future it will be possible to use to determine the costs of the different activities carried out by crustaceans in the field. Another drawback in this sense is the need to record data continuously, which will be mitigated by the development of automated systems discussed earlier.

Lastly, all of these possible future developments, in addition to the techniques currently in use, will benefit unquestionably from the miniaturization of the transmitters and electronic tags used. This has expedited the transfer of the technology used in large-sized animals such as birds and mammals to fishes, and subsequently to invertebrates, and it has served to broaden the range of species and life stages to include small-sized animals. These advancements may lead to the widespread use of these systems as methods of behavioural and physiological 'observation' in the marine environment.

Acknowledgements

Part of the research presented in this paper was funded by the Consellería de Pesca, Marisqueo e Acuicultura of the Xunta de Galicia, the Dirección General de Investigación Científica y Técnica (DGICYT) of the Spanish Ministerio de Educación y Cultura, and the Fundación Caja de Madrid. We are grateful to Dr A. H. Hines for his insights in the use of telemetry with decapods and for the discussion of different aspects of our research projects.

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