



Defensive strategies of European spiny lobster *Palinurus elephas* during predator attack

G. Buscaino^{1,*}, F. Filiciotto¹, M. Gristina², G. Buffa¹, A. Bellante¹, V. Maccarrone¹,
B. Patti¹, S. Mazzola¹

¹Istituto per l'Ambiente Marino Costiero U.O. S. di Capo Granitola — Consiglio Nazionale delle Ricerche, Via del Faro No. 3, 91021 Granitola, TP, Italy

²Istituto per l'Ambiente Marino Costiero U.O. S. di Mazara del Vallo — Consiglio Nazionale delle Ricerche, Via L. Vaccara no. 61, 91026 Mazara del Vallo, TP, Italy

ABSTRACT: The aim of the present work was to reveal the behaviour of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) during encounters with predators. The study was conducted in a tank, exposing lobsters individually or in groups to a single specimen of the European conger eel or the common octopus. The behaviours of the lobsters, their sounds and the behaviours of the predators were recorded using a digital audio-video underwater acquisition system and analysed. A behavioural event not found in literature, dubbed 'Alert' by the authors, was described. The results showed that the most recurrent events were Alert, Point and Whip, which have the function of controlling the predator with the antennae, while maintaining the predator–prey distance. Moreover, a strong association between Tail Flip and Lunge (events that were stimulated in response to an imminent danger to life) with the sounds emitted by lobsters was observed. Significantly more sounds were emitted during the tests with single lobsters compared to grouped lobsters. As a result of the present study, the European conger eel may also be considered a potential natural predator of the European spiny lobster.

KEY WORDS: European spiny lobster · Behaviour · Antipredatory strategies · Common octopus · European conger eel

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Benthic stages of palinurid lobsters are subjected to a wide array of predators: groupers (Eggleston et al. 1997, Quetglas et al. 2001), triggerfish (Barshaw et al. 2003, Briones-Fourzán et al. 2006, Weiss et al. 2008, Lavalli & Herrnkind 2009), sharks (Berry 1971, Eggleston & Lipcius 1992), stingrays and octopus (Berger & Butler 2001).

To minimize the predation risk, which represents the primary source of natural population mortality (Butler & Herrnkind 2000, Butler et al. 2006), lobsters have developed effective defensive strategies for each life-history stage. Defence mechanisms are generally mediated by 2 major strategies (Sih 1985, Brodie et al. 1991): (1) 'predator-avoidance mechanisms' (e.g. crypticity, immobility, nocturnal activity, sheltering) adopted by a lob-

ster before an attack to reduce the risk of predator encounters (Barshaw et al. 2003, Briones-Fourzán et al. 2006, Gristina et al. 2009) and (2) 'antipredator mechanisms' (e.g. escape, aggregation, cooperative defence, weaponry, clinging to the substrate) adopted during an attack to reduce the risk of capture and killing (Vermeij 1982, Sih 1987, Brodie et al. 1991, Spanier et al. 1991, Barshaw & Spanier 1994, Hazlett et al. 2000, Herrnkind et al. 2001, Seitz et al. 2001, Barshaw et al. 2003, Bouwma & Herrnkind 2005, Lind & Cresswell 2005, Briones-Fourzán et al. 2006, Lavalli & Herrnkind 2009). With regards to the 'antipredator mechanisms', several studies have described a range of defensive actions adopted by spiny lobsters to counteract diurnal predators in the open (Herrnkind et al. 2001, Barshaw et al. 2003, Bouwma 2006, Briones-Fourzán et al. 2006, Parsons & Eggleston 2006, Lavalli & Herrnkind 2009). These stud-

*Email: giuseppa.buscaino@cnr.it

ies, carried out both in the field and in mesocosms, have identified a wide set of behavioural actions adopted by spiny lobsters during predator encounters. Within these, the use of antennae probably represents the most effective antipredator weapon for spiny lobsters. In fact, the spinous antennae, with their powerful basal musculature, can be used in a wide array of defensive tactics: to keep the predator at distance ('Point' or 'Parry') or to slap against the predator's body ('Whip' or 'Lunge') (Lavalli & Herrnkind 2009). The use of antennae in combination with rapid contractions of the abdomen musculature ('Tail Flip', 'Rear Back') (Lavalli & Herrnkind 2009), with movement of walking legs ('Pirouette', 'Walk') (Lavalli & Herrnkind 2009) and with cooperative defence strategies ('queue', 'rosette', 'phalanx') (Herrnkind et al. 2001, Briones-Fourzán et al. 2006), confers to spiny lobster a useful tool with which to counteract predator attack during different life-history stages and in several ecological conditions. Furthermore, in combination with antennae sweeping, stridulatory spiny lobsters are able to produce a characteristic loud sound (Moulton 1957, Smale 1974, Mercer 1975, Mulligan & Fischer 1977, Patek 2001, 2002, Bouwma & Herrnkind 2005, 2009).

Despite the wide scientific interest in this topic, the sound-production mechanism of stridulatory decapod crustaceans within the general framework of 'antipredator mechanisms' is not completely understood. Some authors have assumed that lobsters only produce sounds in an antipredatory context (Lindberg 1955, Moulton 1957, Hazlett & Winn 1962, Meyer-Rochow & Penrose 1974, 1976, Patek 2001, 2002, Patek & Oakley 2003, Bouwma & Herrnkind 2009), while others suggest that sounds may be used in social context as well (Moulton 1957, Mercer 1973, 1975). In particular, Bouwma & Herrnkind (2005) and Bouwma (2006) demonstrated that Caribbean spiny lobsters *Panulirus argus* and *P. guttatus* in which the sound-production mechanism had been disabled were attacked and killed more frequently by *Octopus briareus* than spiny lobsters with intact sound-producing structures. Sound emanates from a specialized stridulating organ composed of 2 parts: a movable plectrum attached to the last segment of the antennal peduncle and a rigid file (Patek 2002, Patek & Oakley 2003, Patek & Baio 2007). This organ is located at the base of the long second antennae, which is also the lobster's primary defensive weapon (Patek 2002). To produce sound, the lobster draws the plectrum up the file by moving the antenna base posteriorly.

The European spiny lobster *Palinurus elephas* (Fabricius, 1787) is common along the Mediterranean and northeastern Atlantic coasts (Hunter 1999, Ceccaldi & Latrouite 2000). It is a temperate species living on rocky and coralligenous substrates where micro-caves

and natural protective holes are numerous from approximately 10 to 200 m in depth (Ceccaldi & Latrouite 2000). This species, primarily active at night, represents one of the main targets of Mediterranean artisanal fisheries, and, while catches are now reduced and sporadic, this fishery has a long history (Goñi & Latrouite 2005, Groeneveld et al. 2006). As a result, almost all *P. elephas* populations in the Mediterranean are clearly overexploited (Goñi & Latrouite 2005, Galhardo et al. 2006). Notwithstanding the economic and ecological importance of *P. elephas* in most parts of the Mediterranean coastal area, experimental data on the antipredator mechanisms of *P. elephas* are scanty or absent (Hunter 1999, Goldman & Patek 2002, Barshaw et al. 2003, Patek & Oakley 2003, Gristina et al. 2009).

The aim of the present study was to experimentally reveal the antipredator behaviours of European spiny lobster *Palinurus elephas* in the presence of potential predators with different swimming abilities and attack strategies: the common octopus *Octopus vulgaris* which employs an ambush strategy (Hanlon & Hixon 1980) and the European conger eel *Conger conger* which mainly attacks prey in the open using the acceleration of its undulatory swimming (Sfakiotakis et al. 1999). Both common octopus and European conger eel co-occur with common lobster in the same coastal, rocky habitat, sheltering in natural holes during the day and mainly active at night (Morato et al. 1999). Many octopuses are natural predators of spiny lobsters (Joll 1977, Harrington et al. 2006, Bouwma & Herrnkind 2009, Butler & Lear 2009) and *O. vulgaris* preys on the common spiny lobster *P. elephas* (Quetglas et al. 2001, Goñi & Latrouite 2005). When threatened by octopus in the open, lobsters attempt to escape by using tailflips, darting backwards away from the attacker. As a result, octopus predation on lobsters in the open may be a rare occurrence, while, using their long and flexible arms, octopuses mainly prey on lobsters inside their dens (Weiss et al. 2006, Bouwma & Herrnkind 2009). The European conger eel is considered a voracious predator, eating a variety of species—Clupeidae (especially sardines), cephalopods (cuttlefish, squid, octopus) and crustaceans such as shrimps and small crabs (Cau & Manconi 1984, Morato et al. 1999, O'Sullivan et al. 2004)—and is also known to enter lobster pots (O'Sullivan et al. 2003). Conger eel predation on lobster is mostly anecdotal and lacking experimental evidence; however, we believe that, inhabiting the same habitat, conger eels probably compete with lobster for limited available shelter and simultaneously could represent a menacing predator. We chose to carry out the experiments without any dens, in order to prevent the presence of available shelters from affecting the attack strategies of the 2 selected potential predators.

The research questions were (1) What are the *Palinurus elephas*' anti-predator behaviours during encounters with 2 different predators, and do they differ according to the predator? (2) What are the behavioural events associated with sound production? (3) Are there differences between single and collective defensive strategies?

MATERIALS AND METHODS

Collection and maintenance of animals. The present study was carried out at the Capo Granitola/CNR laboratory (SW Sicily), from May to June 2009. Fifty adult European spiny lobsters *Palinurus elephas* (31 males and 19 females) weighing 193 ± 54 g and measuring 183 ± 25 mm in total length (mean \pm SD), 5 adult European conger eels *Conger conger* weighing 2044 ± 278 g (mean \pm SD) and 5 adult common octopuses *Octopus vulgaris* weighing 1656 ± 168 g (mean \pm SD) were used. All animals were captured between January and February 2008. The European spiny lobsters were captured at from 20 to 25 m depth near Isola delle Femmine (NW Sicily) by fishermen using a commercial trammel net (54 mm inner panel mesh size; 1200 m length). Individuals were transferred to 2 shaded outdoor PVC circular tanks (3.0 m diameter) supplied with a thin layer of sand (about 1 cm depth). The common octopuses and the European conger eels were caught using trammel nets and long lines, respectively, by a commercial fishery at the same location and depths of the lobsters. In the laboratory, octopuses and conger eels were kept in 2 separate outdoor PVC circular tanks (3.0 m diameter) supplied with a thin layer of sand (about 1 cm depth). Temperature and salinity levels were monitored using a multiparametric probe (EC300, VWR International LCC) and were kept constant, at $19.3 \pm 0.78^\circ\text{C}$ (mean \pm SD) and 35.4 ± 0.81 ppt (mean \pm SD), respectively, with a constant flow of seawater provided at a rate of 25 ± 3.7 l min^{-1} (mean \pm SD). The tanks were covered with a dark cloth to reduce the intensity of light radiation. The lobsters were fed crabs and frozen shrimps ad libitum. The octopus and conger eel were fed shrimps and frozen fish (*Boops boops*) ad libitum, but were deprived of food for 5 d before the start of the experimental trials. All animals were kept under natural photoperiods.

The protocols of animal husbandry and experimentation were reviewed and approved in accordance with recommended standards (NRC 1996) and EEC Directive 86/609.

Rationale and experimental procedures. All experiments were carried out in a circular outdoor PVC tank (3.0 m diameter) supplied with a thin layer of sand (about 1 cm depth). Although several authors de-

scribed palinurids as being mainly active at night (MacDiarmid et al. 1991, Hunter 1999), Giacalone et al. (2006) demonstrated intense activity also during the day for *Palinurus elephas*. For this reason, we carried out all the experiments in the afternoon (at approximately 17:00 h), and we stopped them before sunset (20:00 h). To assess the defence behaviour of *P. elephas* during predator attacks, we exposed lobsters, individually and in groups of 4 individuals, to a solitary predator. Ten trials were performed with a single lobster, 5 with an octopus and 5 with a conger eel. Likewise 10 trials (5 by each predator) were performed using groups of 4 lobsters.

The lobsters (individually or in groups) were randomly collected from the holding tanks, assigned to the trials and used in 1 experiment only to meet the assumption of experimental independence. Each predator individual was used twice

Lobsters (individually or in groups) were released in the centre of the experimental tank, without any shelter, and after 1 h of habituation, the trial was started. After the 1 h of habituation and in the absence of any predator, each lobster's behaviour was monitored for another 1 h (control phase). A predator (octopus or conger eel) was then released into a cylindrical tank (80 cm diameter, 40 cm high) in the centre of the arena; after 10 s, the tank was removed and lobster (individually or in groups) and predator behaviour was monitored for a further 1 h (test phase) (Fig. 1).

The behavioural repertoires of the spiny lobster *Palinurus elephas* and its predators *Octopus vulgaris*, *Conger conger* during predator-prey encounters were derived from analysis of the videotapes. These behavioural patterns, recorded during each trial, were assigned to behavioural categories following the general scheme proposed by Lavalli & Herrnkind (2009), modified by the authors for the present study (Fig. 2).

Data monitoring and acquisition system. To avoid disturbing the animals inside the experimental tank, a

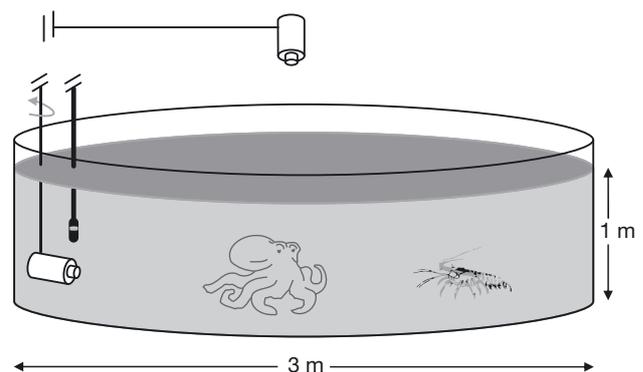


Fig. 1. Schematic representation of experimental tank equipped with a hydrophone and video cameras

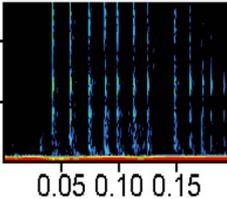
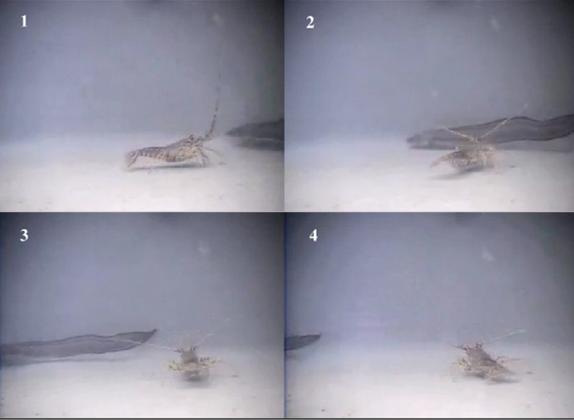
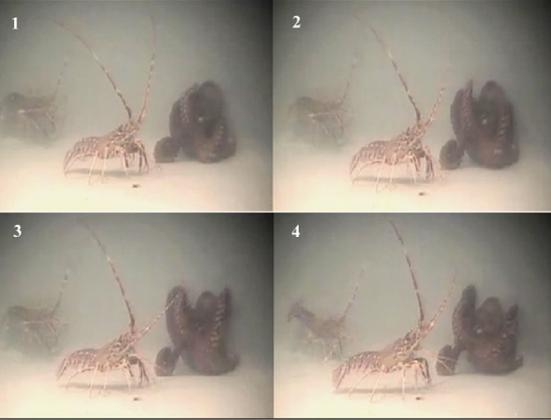
Lobster behavioural event		
Alert	Point	Parry
		
<p>The lobster points towards the direction of predator with both the antennae, raising telson and stretching the legs. Lobster's body (including the antennae) doesn't move except for the flicking of the antennules.</p>	<p>One or both antennae of the lobster move towards, or are held in, the direction of the predator. No contact is made. Lobster doesn't raise the telson and the legs.</p>	<p>The tip or side of an antenna of the lobster makes contact with some part of the predator; can include swiping the predator or holding one or both antennae against the predator to keep it at a distance.</p>
Tail Flip	Lunge	Sound Emission
		
<p>The lobster makes a rapid flexion of the extended abdomen, one or more times, which results in propelling the lobster to a new location away from the predator.</p>	<p>The lobster's antennae are swept together rapidly in front of the lobster and the body rapidly moves forward towards the predator, by the use of the legs and/or the rapidly undulating telson; the antennae may or may not make contact.</p>	<p>The lobster emits a single or multiple audible acoustic signal(s) (the spectrogram of an audible rasp; X is the time in seconds, Y is the frequency in kHz).</p>
Pirouette		Whip
		
<p>The lobster turns on the spot ($\geq 180^\circ$) while keeping the antennae and anterior of the body directed at the attacking predator.</p>		<p>The lobster strikes the predator with either one or both antennae without an associated forward movement of the body or simply pushes the predator away using the antennae.</p>
Lobster status		
Walking	The lobster uses its legs to move itself to another location.	
Resting	The lobster maintains its position. Antennae could move.	
Predator action		
Attack	The predator moves directly towards the lobster to within one antenna's length, approaching, handling or with damaging action.	

Fig. 2. *Palinurus elephas*. Description of the behavioural events and states of the European spiny lobster and predator action

laboratory was located 5 m away from the tank, in which the equipment required for audio-video monitoring and recording was placed.

The video monitoring was carried out using 2 cameras. One low light camera (Model CCD colour camera 1090/205, Urmet Domus SPA) was placed 3 m above the centre of the tank, for an overall view of the experimental space. A low light underwater camera (Model RE-BCC6L, DSE), which could be rotated 160°, was positioned on the bottom of the tank, on the side nearest the audio-video monitoring laboratory, in order to obtain a side view of the predators and lobsters.

Sound emissions by the lobsters were recorded using a hydrophone (Model 8104, Bruel & Kjer; receiving sensitivity of $-205 \text{ dB re } 1 \text{ V } \mu\text{Pa}^{-1} \pm 4.0 \text{ dB}$ in the frequency band 0.1 Hz to 80 kHz) connected to a preamplifier (VP1000, Reson; 1 MHz bandwidth single-ended voltage). The signals from the cameras and the hydrophone were synchronized, digitized, and stored using a DAQ card (Model DV-RT4 Real Time, D-Vision) managed by custom-written software (Model DSE, D-Vision).

Audio-video recording analysis. The synchronized audio-video data were analysed in continuous mode. The behaviour of the lobsters and predators was recorded for 2 h: 1 h for the control and 1 h for the test phase. Moreover, for lobsters, we distinguished the behavioural states and events, including movements/postures and audible sound emissions (see Fig. 2).

With regards to the behavioural states, we analysed mobility and clustering. As an indicator of mobility, in trials with individual lobsters, the percentage of time spent walking or resting was assessed. In trials with groups of lobsters, the percentage time spent in different clustering conditions was recorded as follows: Cluster 4 (each lobster was in contact with another by any portion of the body), Cluster 3 (3 lobsters were in contact by any portion of their body and 1 individual was isolated), and no cluster (a cluster was made up of 2 lobsters at most).

Statistical analysis. Data were tested for goodness of fit to the normal distribution using the chi-squared test. Since the data were not normally distributed, non-parametric tests were used to compare different variables within (control vs. test) and between trials. The Kruskal-Wallis, Mann-Whitney *U* and Wilcoxon non-parametric tests were used to evaluate differences in the following variables:

- the number of attacks by the octopuses and the conger eels against the lobsters individually or in groups;
- the mobility of single lobsters during the control and test phases;
- the clustering condition of lobsters in groups during the control and test phases;
- the number of behavioural events of lobsters per capita in all trial types.

Moreover, for each test type (single lobster vs. octopus; single lobster vs. conger eel; lobsters in group vs. octopus; lobsters in group vs. conger eel), a linear regression model ($y = a + bx$) was applied to the total number of predator attacks per trial (regressor) and to the total number of behavioural events shown by lobsters per trial (regressand). In the cases of significant positive relation ($p < 0.05$), analysis of covariance (ANCOVA) was used to compare the mean number of events between the different test types, using the number of predator attacks as the covariate.

A p -value of <0.05 was considered to indicate statistical significance. All statistical analyses were performed using the STATISTICA 7.0 software package.

RESULTS

Predator attacks

Conger eels *Conger conger* launched a significantly higher number of attacks on lobsters *Palinurus elephas* (both individuals and groups) than the octopus *Octopus vulgaris* (Mann-Whitney *U*-test; $p < 0.01$) (Fig. 3). The octopus showed a preference for attacking grouped lobsters (Mann-Whitney *U*-test; $p < 0.05$) compared to single lobsters, while the conger eel did not show any significant preference (Mann-Whitney *U*-test; $p > 0.05$), even though the number of attack towards grouped lobsters was higher (Fig. 3). Nevertheless, with regards to the median number of predator attacks per lobster, the grouped lobsters were attacked significantly less often than single lobsters (Mann-Whitney *U*-test, $p < 0.05$).

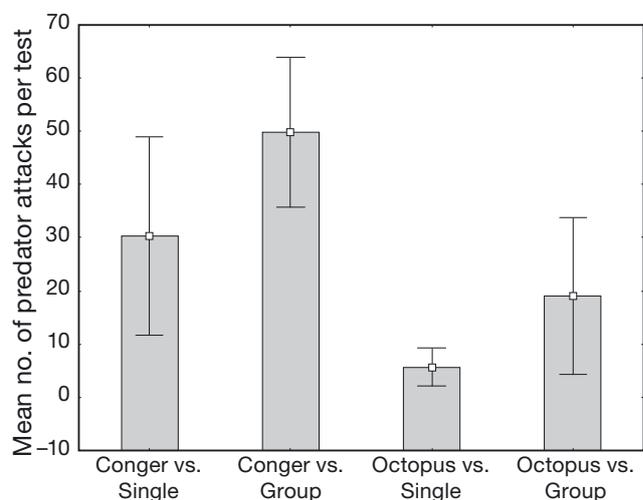


Fig. 3. *Palinurus elephas*. Mean number of attacks ($n \text{ h}^{-1} \pm \text{SD}$) by conger eels *Conger conger* ($n = 5$) and common octopuses *Octopus vulgaris* ($n = 5$) per test with single ($n = 10$) or grouped lobsters ($n = 40$)

No lobsters were killed during any of the experiments, whilst the amputation of antennae or legs was recorded 3 times only in the trials performed with single lobsters (in 1 case with the octopus and in the other 2 cases with the conger eel).

Behavioural state of lobsters

Mobility of single lobsters

In the control period, lobsters remained in the resting state for $47 \pm 13\%$ (mean \pm SE) of the time and in the walking state for $53 \pm 13\%$ (mean \pm SE) of the time, with a mean number of state changes of 7 ± 10 (mean \pm SE).

After predator introduction there was an increase in the resting state ($64 \pm 7\%$; mean \pm SE) compared to walking ($36 \pm 7\%$; mean \pm SE). In particular, in tests with octopuses, there was a statistically significant prevalence of the resting state compared to walking (Wilcoxon, $p < 0.05$). Moreover, an increase in status changes ($13 \pm 5\%$; mean \pm SE) was observed during these tests.

Clustering

During the control period, there was a prevalence of lobsters in Cluster 4 ($48 \pm 12\%$, mean \pm SE), compared to Cluster 3 ($36 \pm 10\%$; mean \pm SE) and no cluster ($16 \pm 7\%$; mean \pm SE) states. In the comparison between the tests with conger eel and octopus, the clustering of lobsters did not show any significant differences (Wilcoxon test, $p > 0.05$). In the presence of predators, there was a reduction in the Cluster 4 ($28 \pm 12\%$; mean \pm SE) and Cluster 3 ($27 \pm 6\%$; mean \pm SE) state and an increase in the no-cluster state ($45 \pm 10\%$; mean \pm SE). In particular, in the tests with octopuses, there were significant differences between the Cluster 4 and no-cluster states (Wilcoxon test, $p < 0.05$) and between the Cluster 4 and Cluster 3 states (Wilcoxon test, $p < 0.05$).

Behavioural events of lobsters

Only after introduction of the predator into the experimental tank did lobsters exhibit the full range of behavioural actions described by Lavalli & Herrnkind (2009). We recorded an undescribed behavioural event that we named 'Alert': the lobster faces towards the predator and flicks the antennules as though detecting the predator odours. The Alert differs from the

Point behaviour because the lobster raises the telson and stretches its legs without movement of the body (except for the antennules) (see Fig. 2).

The most recurrent event was the Alert (with a value for all tests of 13.2 ± 3.6 ; mean number per capita per hour \pm SD) (Fig. 4). Secondary behaviours were the Point (12.9 ± 3.2) and the Whip (11.6 ± 3.9) (Fig. 4). The Whip was not observed during the tests with single lobsters with octopus (and was rarely observed in tests of groups against an octopus: 1.4 ± 0.8 h; mean \pm SD) (Fig. 4). Similarly, the Lunge has never been recorded in tests with octopuses (Fig. 4). The Parry was also rarely observed in tests with octopuses (Fig. 4).

Among the events arising in response to imminent life-threatening danger (Bouwma & Herrnkind 2009, Lavalli & Herrnkind 2009), and/or characterized by high mobility, were the Sound Emission (6.02 ± 2.20), the Tail Flip (4.88 ± 1.53) and the Lunge (0.85 ± 0.42) (Fig. 4).

When comparing the behavioural events between all test typologies (multiple comparisons, Kruskal-Wallis test), no significant differences in behavioural responses per capita were observed, except for the Whip, which was significantly more frequent in single lobsters with conger eels than in those with octopuses ($p < 0.01$), and the Parry, which was more frequent in lobsters in groups with conger eels than in single lobsters with octopuses ($p < 0.05$).

In total, 2433 behavioural events were recorded, of which 239 (10%) were Sound Emissions. All Sound Emissions occurred in association with the Lunge, Tail Flip, Parry, Whip and Point behaviours. Table 1 shows the total number of behavioural events, with the percentage associated with Sound Emissions. The Tail Flip showed the highest percentage (76%) of associations with Sound Emissions.

Only in tests with single lobsters (both with conger eels and octopuses) were the relations between attacks and movement/posture events positively significant (Fig. 5). In all tests, the relations between the attacks and the Sound Emissions were positively significant, except for single lobsters versus octopuses (Fig. 5).

Table 1. *Palinurus elephas*. Number of behavioural events of lobsters, and percentage of associations with audible sounds. Data in parentheses are the percentage of events associated with Sound Emission

	Tail Flip	Lunge	Parry	Whip	Point
Total number of events	185 (75.7)	15 (53.3)	386 (13.5)	352 (10.5)	595 (0.3)
Events with conger eel	104 (76.9)	15 (53.0)	377 (13.8)	328 (11.3)	491 (0.2)
Events with octopus	81 (75.3)	0	9 (0.0)	24 (0.0)	104 (1.0)

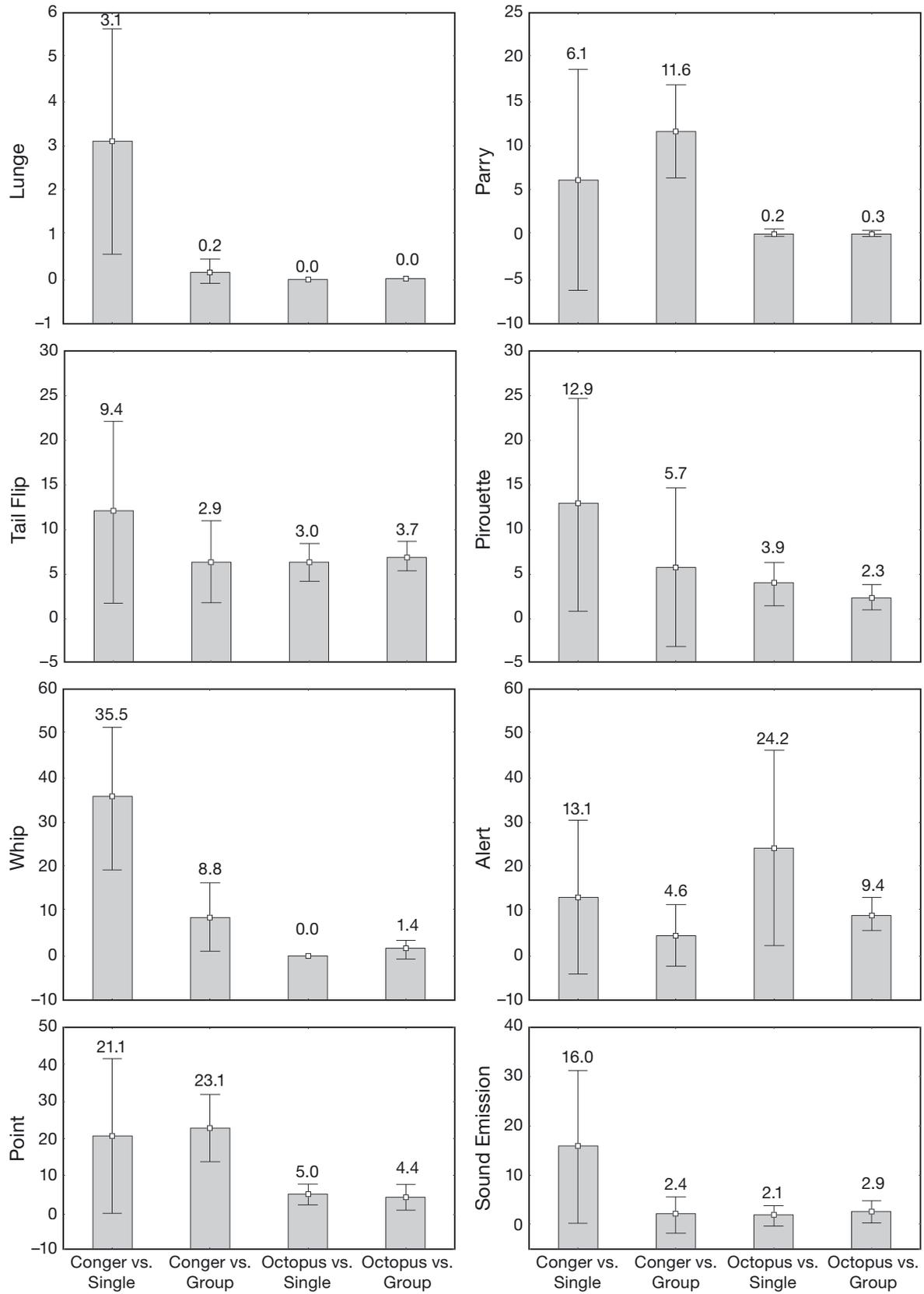


Fig. 4. *Palinurus elephas*. Mean number of antipredator behavioural events ($n\ h^{-1} \pm SD$) of lobsters per capita per test type

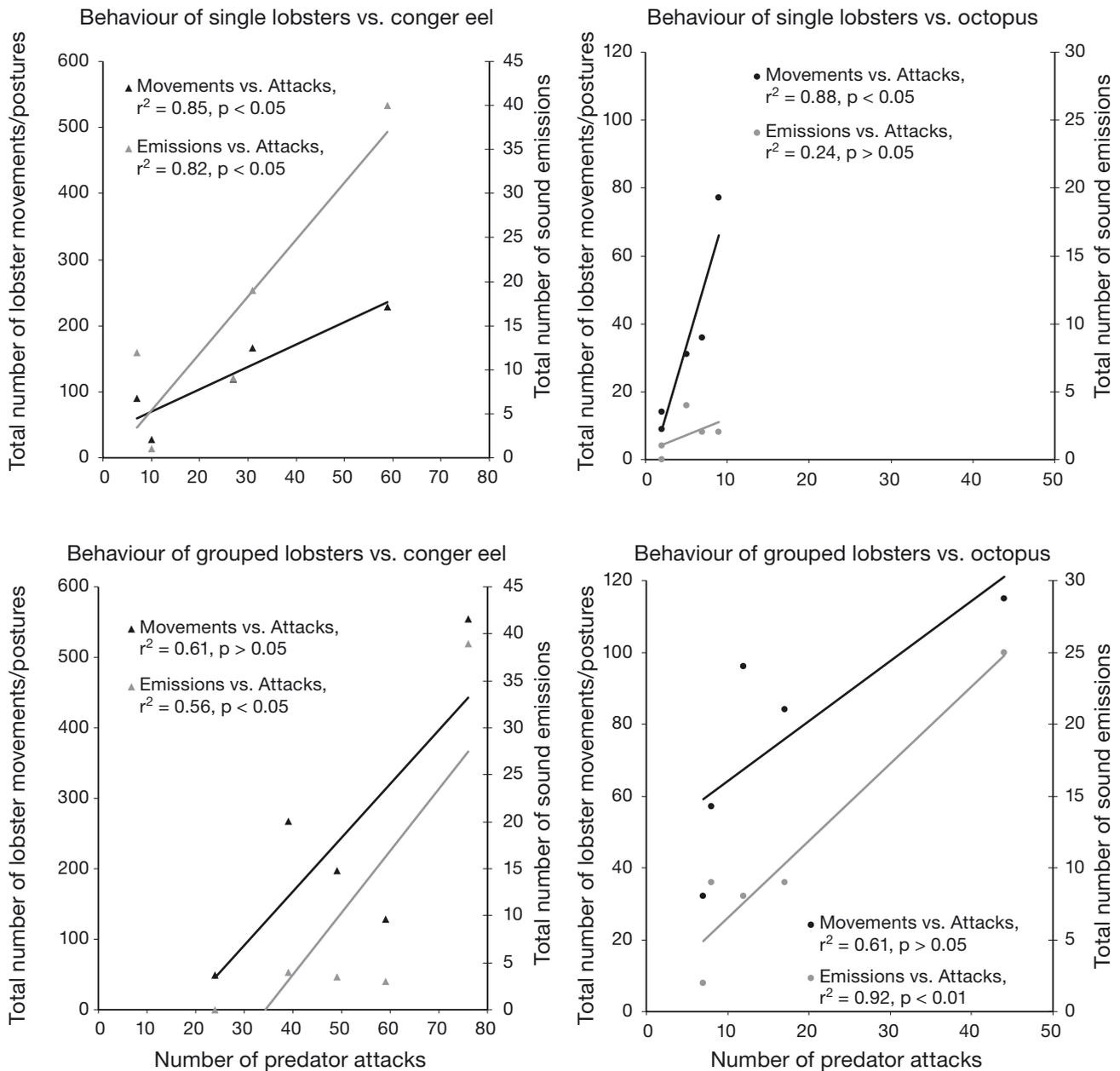


Fig. 5. *Palinurus elephas*. Linear relation between the total number of predator attacks (left panels: conger eels *Conger conger*; right panels: common octopus *Octopus vulgaris*) and the total number of behavioural events of lobsters, divided into movements/postures (left y-axis) and sound emissions (right y-axis) in tests with single and grouped lobsters. The key shows p-values and r^2 -values of the linear relations

In tests with single lobsters versus conger eels, the number of Sound Emissions in relation to the number of predator attacks was significantly higher than in tests with lobsters in groups (ANCOVA: $F_{(1,7)} = 9.4776$, $p < 0.05$).

Moreover, in tests with lobsters in groups, the number of sounds emitted in response to attack by the octopus was greater than that emitted with the conger eel (ANCOVA: $F_{(2,6)} = 8.6516$, $p < 0.05$).

DISCUSSION

Many palinurids adopt antipredator strategies encompassing both 'predator-avoidance' and 'antipredator mechanisms'. Most spiny lobster taxa exhibit gregarious behaviour—sharing shelters (Childress & Herrnkind 1997, 2001), aggregating in complex, coordinated formations (Herrnkind et al. 2001) and sensing olfactory alarm signals (Briones-Fourzán et al. 2008,

Shabani et al. 2008). In addition, spiny lobsters can use a wide range of antipredator mechanisms, such as escaping to safe distances from predators (Briones-Fourzán et al. 2006), pointing or parrying the antennae against the predator to keep it at a distance, scraping the predators by sweeping the spinous antennae together (Lavalli & Herrnkind 2009), clinging to the substrate and avoiding shelters infused with predator scent (Berger & Butler 2001, Briones-Fourzán et al. 2008). However, despite the considerable scientific information on this subject for several crustacean decapod species worldwide, our knowledge of how palinurids in general, and *Palinurus elephas* in particular, adapt their defensive strategies to predators with different hunting strategies still remains sketchy.

In the present study, we attempted to describe the European spiny lobster's skill in modifying its defensive mechanisms when exposed in the open to predators with different attack strategies. The experimental trials were performed in captive conditions in a relatively small tank (3 m in diameter). To ensure that the presence of shelters could not benefit 1 of the 2 tested predators, no refuges were provided in the experimental tanks.

Both predators attacked lobsters in groups more often than single lobsters. However, the mean number of attacks suffered per capita by lobsters in groups was significantly lower than the number suffered by single specimens. Similar results were obtained by Lavalli & Spanier (2001) with respect to Mediterranean slipper lobsters. This may be attributable to the effectiveness of the group antipredator strategies reported by several authors (Barshaw et al. 2003, Briones-Fourzán et al. 2006, Lavalli & Herrnkind 2009). The number of attacks by conger eels was significantly higher than that by octopuses. This phenomenon could be explained by the different attack strategies of the 2 predators: conger eels, characterized by undulatory swimming, are more mobile than octopus, and, in confined spaces, this may increase the chances of stumbling upon lobsters, with a direct impact on the number of attacks. In contrast, the hunting strategies of *Octopus vulgaris*, which mainly prey on lobsters inside their dens, seem to be less efficient in the open (Weiss et al. 2006, Bouwma & Herrnkind 2009). Although the literature contains no clear information about the predator function of conger eels against spiny lobsters, these results show that this species could represent a potential predator of the European spiny lobster.

During the control period, single lobsters spent the majority of their time Walking, with a few variations. This behaviour, probably relating to monitoring/exploration of the surrounding space and perhaps also to the lack of available shelters, showed substantial changes when a predator was introduced into the tank.

In fact, when single lobsters were exposed to an octopus, they spent most of the time freezing their bodies and antennae (pointed towards the predator), raising telsons, stretching legs and flicking antennules to detect predator odors (the 'Alert' posture, described for the first time herein). When octopus attack the potential prey and extend their tentacles in an attempt to grasp and catch, lobsters generally react by pointing their antennae (Point), pirouetting and, above all, tail-flipping. The rapid flexion of the extended abdomen, one or more times, propels the lobster into a new location, ensuring that the octopus cannot grip the carapace and abdomen with its arms. Lobsters try to establish and maintain a safe distance from the octopus, avoiding direct contact with the predator. Through this mechanism, lobsters can circumvent octopus attacks in the open, thus confirming the observation that 'predation on lobsters in the open under natural conditions by octopus may be a rare occurrence' (Bouwma & Herrnkind 2009, p. 8). Conversely, an octopus, introducing its long arms into dens, can easily capture and kill lobsters when they are sheltered in a confined space, preventing escape. Due to the behavioural actions performed by single lobsters when exposed to octopus, the low number of sounds emitted was expected. In fact, the defensive strategy described for lobsters—mainly based on keeping the predator at a safe distance—reduces the behavioural actions coincident with stridulation (Lunge, Parry). Furthermore, the lack of direct contact (and of a probable capture) between lobsters and octopuses reduces the Sound Emissions, no matter what their functional significance (aposematic, calling for help from conspecifics, alerting conspecifics to danger, attracting another predator to interfere with the attacker) (Smith 1986, Driver & Humphries 1988, Bouwma 2006, Bouwma & Herrnkind 2009, Klump & Shalter 2010).

To counteract the hunting strategies of conger eel, single *Palinurus elephas* change their defensive strategies. The time spent in the Alert posture previously described for the octopus–single lobster interaction appears strongly reduced, and, on the contrary, lobsters assume a more active, defensive behaviour. Whip, Point, Tail Flip and Parry are more frequent behavioural actions adopted by lobsters to circumvent the threat posed by conger eels. In general, lobsters shift their body to face the predator, trying to keep their antennae in a position to threaten the fish.

When attacked by a conger eel, single lobsters tend to use their antennae to keep the predator at a distance, to strike the predator (Whip), or to sweep their antennae rapidly in front of the predator to scrape or scratch it (Lunge). This defensive behaviour is similar to that described by Lavalli & Herrnkind (2009) for triggerfish *Balistes carolinensis* versus *Panulirus argus*.

Moreover, the defensive strategy adopted by single lobsters when exposed to conger eels is characterised by a high level of Sound Emission. The numerous instances of Sound Emission can be explained by the frequent use of Tail Flip and Lunge behaviours, actions coincident with stridulation. Moreover, the long snake-like body of the conger eel and its undulatory swimming (Sfakiotakis et al. 1999), probably, compel lobsters, during an attack, to more often repeat defensive behavioural actions (Lunge and Whip) linked to Sound Emissions.

When grouped lobsters were threatened by octopus, they left the group (Cluster 4) joined during the control phase and individually sought a new location away from the predator. In this situation, grouped lobsters suffered a higher mean number of attacks compared to single lobsters, but a lower number of attacks per capita. Grouped lobsters seem to abandon the potential anti-predatory benefits of group formation, preferring to adopt individualistic strategies. The no-cluster strategy in grouped lobsters may be adopted to avoid focusing the attention of predators on a specific place, leading to uncertainty in the choice of target prey, as in many gregarious fish and crustacean species (Brock & Riffenburgh 1960, O'Brien 1988, Magurran 1990). The adopted defensive strategy allows each member of a group to expend less effort (fewer defensive actions) compared with solitary individuals (Lavalli & Herrnkind 2009) and seems to be efficient, since the mean number of attacks per capita suffered by grouped lobster specimens was lower than that suffered by single specimens.

The grouped lobsters exposed to the conger eel also suffered a higher mean number of attacks. Again, the grouped specimens abandoned the cooperative defence advantages provided by compact formations and used their antennae individually to keep the predator at a safe distance (Point and Parry). This observation suggests that aggregation and cooperation do not represent a fundamental defence mechanism against conger eel hunting strategies and do not confirm the findings of other studies on predator–prey interactions between spiny lobster and fish (Herrnkind et al. 2001, Barshaw et al. 2003, Briones-Fourzàn et al. 2006, Lavalli & Herrnkind 2009).

The different defence strategies adopted by grouped lobsters against octopus versus conger eel seem to also affect the use of sound production. In grouped spiny lobsters both predators stimulated a number of Sound Emissions linearly related with the number of predator attacks. However, analysis of Sound Emissions in relation to the number of predator attacks clearly shows that grouped lobsters emit significantly more sounds in the presence of octopuses than of conger eels.

The significantly higher number of sounds emitted by single lobsters in comparison with grouped lobsters when attacked by conger eels seems to confirm the effectiveness of the defence strategies adopted by lobsters against the fish (Barshaw et al. 2003, Briones-Fourzàn et al. 2006, Lavalli & Herrnkind 2009). Probably, when grouped lobsters face the conger eel, they adopt a strategy of diffuse attention, allowing them to minimize the behavioural events associated with stridulation (Tail Flip, Lunge, Parry, Whip).

The results of the present study allow us to describe the mechanisms lobsters use to counteract predators with different hunting techniques. However, we know that laboratory conditions do not completely reflect field conditions (Miller & Addison 1995, Zhou & Shirley 1997). In particular, due to the homogeneous size of the lobsters and of the predators employed in our trials, we could not assess how the relative size of competitors affects the defensive behaviour of *Palinurus elephas* and, conversely, the hunting strategies of the predators. In this regard, Lavalli & Herrnkind (2009) underscored that individual size conferred an advantage to solitary *P. argus*, so that larger animals suffered fewer damaging bites when attacked by triggerfish *Balistes capricus*. In addition, we worked on inexperienced predators, with a probable low level of aggressiveness (although 3 amputation events of antennae/legs were recorded). Lavalli & Herrnkind (2009) suggested that, by feeding the predator with lobster during the training period, the predatory skill level of *B. capricus* was strongly increased. Although previous caveats have to be considered in the interpretation of results, we believe that the tested lobsters, both solitary and grouped, showed a wide range of defensive strategies.

These results permit us to evaluate the defensive behaviour and skills of *Palinurus elephas* in adapting its antipredator mechanisms to the different hunting strategies of predators. (1) In the present study we have described for the first time the behavioural event designated Alert. (2) We have also shown that, above all in the presence of octopus, the effectiveness of the 'controlling' behavioural event (more frequent use of Alert, Point and Whip) reduces the frequency of 'last resort' behavioural events (i.e. Tail Flip, Lunge), which are associated with greater Sound Emissions. (3) Furthermore, the antipredator strategies adopted by solitary lobsters versus groups of lobsters appear to change in order to counteract predators with different hunting techniques. (4) Finally, we have demonstrated that conger eels perform more attacks than octopuses and are a potential natural predator of European spiny lobster.

Acknowledgements. We are grateful to 4 anonymous reviewers for the constructive comments that helped improve this manuscript and to the editor, James McClintock, for his patience.

LITERATURE CITED

- Barshaw DE, Spanier E (1994) Anti-predator behaviors of the Mediterranean slipper lobster, *Scyllarides latus*. *Bull Mar Sci* 55:375–382
- Barshaw DE, Lavalli KL, Spanier E (2003) Offense versus defense: response of three morphological types of lobsters to predation. *Mar Ecol Prog Ser* 256:171–182
- Berger DK, Butler MJ (2001) Octopuses influence den selection by juvenile Caribbean spiny lobster. *Mar Freshw Res* 52:1049–1053
- Berry PF (1971) The biology of the spiny lobster *Panulirus homarus* (Linnaeus) off the east coast of southern Africa. Invest Rep no. 28. Oceanography Research Institute, Durban
- Bouwma P (2006) Aspects of antipredation in *Panulirus argus* and *Panulirus guttatus*: behavior, morphology, and ontogeny. PhD dissertation, Florida State University, Tallahassee, FL
- Bouwma PE, Herrnkind WF (2005) Spiny lobsters combine weaponry with sound to 'teach' predators not to attack. In: Proc 34th annual benthic ecology meeting, April 6–10, 2005, Virginia Institute of Marine Science, Williamsburg, VA, p 27 (Abstract)
- Bouwma PE, Herrnkind WF (2009) Sound production in Caribbean spiny lobster *Panulirus argus* and its role in escape during predatory attack by *Octopus briareus*. *NZ J Mar Freshw Res* 43:3–13
- Briones-Fourzán P, Pérez-Ortiz M, Lozano-Álvarez L (2006) Defense mechanisms and antipredator behavior in two sympatric species of spiny lobsters, *Panulirus argus* and *P. guttatus*. *Mar Biol* 149:227–239
- Briones-Fourzán P, Candela J, Lozano-Álvarez E (2008) Post-larval settlement of the spiny lobster *Panulirus argus* along the Caribbean coast of Mexico: patterns, influence of physical factors, and possible sources of origin. *Limnol Oceanogr* 53:970–985
- Brock VE, Riffenburgh RH (1960) Fish schooling: a possible factor in reducing predation. *J Cons Int Explor Mer* 25:307–317
- Brodie ED Jr, Formanowicz DR Jr, Brodie ED III (1991) Predator-avoidance and antipredator mechanisms: distinct pathways to survival. *Ethol Ecol Evol* 3:73–77
- Butler MJ IV, Herrnkind WF (2000) Puerulus and juvenile ecology. In: Phillips BF, Kittaka J (eds) Spiny lobsters: fisheries and culture. Blackwell, Oxford, p 276–301
- Butler MJ IV, Lear JA (2009) Habitat-based intraguild predation by Caribbean reef octopus *Octopus briareus* on juvenile Caribbean spiny lobster *Panulirus argus*. *Mar Ecol Prog Ser* 386:115–122
- Butler MJ IV, Steneck RS, Herrnkind WF (2006) Juvenile and adult ecology. In: Phillips BF (ed) Lobsters: biology, management, aquaculture and fisheries. Blackwell, Oxford, p 263–309
- Cau A, Manconi P (1984) Relationship of feeding, reproductive cycle and bathymetric distribution in *Conger conger*. *Mar Biol* 81:147–151
- Ceccaldi HJ, Latrouite D (2000) The French fisheries for the European spiny lobster *Palinurus elephas*. In: Phillips BF, Kittaka J (eds) Spiny lobster fisheries and culture, 2nd edn. Blackwell, Oxford, p 200–209
- Childress MC, Herrnkind WF (1997) Den sharing by juvenile spiny lobsters (*Panulirus argus*) in nursery habitat: Cooperation or coincidence? *Mar Freshw Res* 48:751–758
- Childress MJ, Herrnkind WF (2001) The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Anim Behav* 62:465–472
- Driver PM, Humphries N (1988) Protean behavior: the biology of unpredictability. Oxford University Press, Oxford
- Eggleston DB, Lipcius RN (1992) Shelter selection by spiny lobster under variable predation risks, social conditions, and shelter size. *Ecology* 73:992–1011
- Eggleston DB, Lipcius RN, Grover JJ (1997) Predator and shelter-size effects of coral reef fish and spiny lobster prey. *Mar Ecol Prog Ser* 149:43–59
- Galhardo AM, Serafim P, Castro M (2006) Aspects of the biology and fishery of the European spiny lobster (*Palinurus elephas*) from the southwest coast of Portugal. *J Crustac Biol* 26:601–609
- Giacalone VM, D'Anna G, Pipitone C, Badalamenti F (2006) Movements and residence time of spiny lobsters, *Palinurus elephas* released in a marine protected area: an investigation by ultrasonic telemetry. *J Mar Biol Assoc UK* 86:1101–1106
- Goldman JA, Patek SN (2002) Two sniffing strategies in palinurid lobsters. *J Exp Biol* 205:3891–3902
- Goñi R, Latrouite D (2005) Review of the biology, ecology and fisheries of *Palinurus* species of European waters: *Palinurus elephas* (Fabricius, 1787) and *Palinurus mauritanicus* (Gruvel, 1911). *Cah Biol Mar* 46:127–142
- Gristina M, Fiorentino F, Garofalo G, Badalamenti F (2009) Shelter preference in captive juveniles of European spiny lobster *Palinurus elephas* (Fabricius, 1787). *Mar Biol* 156:2097–2105
- Groeneveld JC, Goni R, Latrouite D (2006) *Palinurus* species. In: Phillips BF (ed) Lobsters: biology, management, aquaculture and fisheries. Blackwell, Oxford, p 385–411
- Hanlon RT, Hixon RF (1980) Body patterning and field observations of *Octopus burryi* Voss, 1950. *Bull Mar Sci* 30:749–755
- Harrington JJ, Semmens JM, Gardner C, Frusher SD (2006) Predation of trap-caught southern rock lobsters, *Jasus edwardsii* (Hutton, 1875), in Tasmanian waters by the Maori octopus, *Octopus maorum* (Hutton, 1880): spatial and temporal trends. *Fish Res* 77:10–16
- Hazlett BA, Winn HE (1962) Sound production and associated behavior of Bermuda crustaceans (*Panulirus*, *Gonodactylus*, *Alpheus*, and *Synalpheus*). *Crustaceana* 4:25–38
- Hazlett BA, Bach CE, McLay C, Thacker RW (2000) A comparative study of the defense syndromes of some New Zealand marine Crustacea. *Crustaceana* 73:899–912
- Herrnkind WF, Childress MJ, Lavalli K (2001) Cooperative defense and other benefits among exposed spiny lobsters: inferences from group size and behaviour. *Mar Freshw Res* 52:1113–1124
- Hunter E (1999) Biology of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) (Decapoda, Palinuridea). *Crustaceana* 72:545–565
- Joll LM (1977) The predation of pot-caught western rock lobster (*Panulirus lobgipes cygnus*) by octopus. Rep. No. 29, Dept. of Fisheries and Wildlife, Perth, WA
- Klump GM, Shalter MD (2010) Acoustic behaviour of birds and mammals in the predator context; I. Factors affecting the structure of alarm calls. II. The functional significance and evolution of alarm signals. *Z Tierpsychol* 66:189–226
- Lavalli KL, Herrnkind WF (2009) Collective defense by spiny lobster (*Panulirus argus*) against triggerfish (*Balistes capricus*): effects of number of attackers and defenders. *NZ J Mar Freshw Res* 43:15–28
- Lavalli KL, Spanier LE (2001) Does gregarious behavior function as an anti-predator mechanism in Mediterranean slipper lobster, *Scyllarides latus*? *Mar Freshw Res* 52:1133–1143

- Lind J, Cresswell W (2005) Determining the fitness consequences of antipredation behavior. *Behav Ecol* 16: 945–956
- Lindberg RG (1955) Growth, population dynamics and field behavior in the spiny lobster, *Panulirus interruptus* (Randall). *Univ Calif Publ Zool* 59:157–248
- MacDiarmid AB, Hickey B, Maller RA (1991) Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *J Exp Mar Biol Ecol* 147:185–205
- Magurran AE (1990) The adaptive significance of schooling as an anti-predator defence in fish. *Ann Zool Fenn* 27:51–66
- Mercer P (1973) Studies on the spiny lobsters (Crustacea: Decapoda: Palinuridae) of the west coast of Ireland, with particular reference to *Palinurus elephas* Fabricius, 1787. PhD thesis, University College, Galway
- Mercer JP (1975) Spiny lobster *Panulirus vulgaris* (Latreille) on the west coast of Ireland. *Proc Challenger Soc* 4: 124–125
- Meyer-Rochow VB, Penrose JD (1974) Sound and sound emission apparatus in puerulus and postpuerulus of the western rock lobster *Panulirus longipes*. *J Exp Zool* 189:283–289
- Meyer-Rochow VB, Penrose JD (1976) Sound production by the western rock lobster *Palinurus longipes* (Milne Edwards). *J Exp Mar Biol Ecol* 23:191–209
- Miller RJ, Addison JT (1995) Trapping interactions of crabs and American lobster in laboratory tanks. *Can J Fish Aquat Sci* 52:315–324
- Morato T, Solà E, Gros MP, Menezes G (1999) Diets of fork-beard (*Phycis phycis*) and conger eel (*Conger conger*) off the Azores during spring of 1996 and 1997. *Arquipel Bull Univ Azores Life Mar Sci* 17A:51–64
- Moulton JM (1957) Sound production in the spiny lobster *Palinurus Argus* (Latreille). *Biol Bull (Woods Hole)* 113:286–295
- Mulligan BE, Fischer RB (1977) Sounds and behavior of the spiny lobster *Panulirus argus* (Latreille, 1804) (Decapoda, Palinuridae). *Crustaceana* 32:185–199
- NRC (National Research Council) (1996) Guide for the care and use of laboratory animals. National Academy Press, Washington, DC
- O'Brien DP (1988) Direct observations of clustering (schooling and swarming) behaviour in mysids (Crustacea: Mysidacea). *Mar Ecol Prog Ser* 42:235–246
- O'Sullivan S, Moriarty C, FitzGerald RD, Davenport J, Mulcahy MF (2003) Age, growth and reproductive status of the European conger eel, *Conger conger* (L.) in Irish coastal waters. *Fish Res* 64:55–59
- O'Sullivan S, Moriarty C, Davenport J (2004) Analysis of the stomach contents of the European conger eel *Conger conger* in Irish waters. *J Mar Biol Assoc UK* 84:823–826
- Parsons DM, Eggleston DB (2006) Human and natural predators combine to alter behavior and reduce survival of Caribbean spiny lobster. *J Exp Mar Biol Ecol* 334:196–205
- Patek SN (2001) Spiny lobsters stick and slip to make sound. *Nature* 411:153–154
- Patek SN (2002) Squeaking with a sliding joint: mechanics and motor control of sound production in palinurid lobsters. *J Exp Biol* 205:2375–2385
- Patek SN, Baio JE (2007) The acoustic mechanics of stick-slip friction in the California spiny lobster (*Panulirus interruptus*). *J Exp Biol* 210:3538–3546
- Patek SN, Oakley TH (2003) Comparative tests of evolutionary trade-offs in a palinurid lobster acoustic system. *Evolution* 57:2082–2100
- Quetglas A, Reñones O, Goñi R (2001) Trophic interactions among grouper (*Epinephelus marginatus*), octopus (*Octopus vulgaris*) and red lobster (*Palinurus elephas*) in the western Mediterranean. *Rapp Comm Int Explor Sci Mer Médit* 36:310
- Seitz RD, Lipcius RN, Hines AH, Eggleston DB (2001) Density dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology* 82:2435–2451
- Sfakiotakis M, Lane CM, Davis BC (1999) Review of fish swimming modes for aquatic locomotion. *IEEE J Oceanic Eng* 24:237–252
- Shabani S, Kamio M, Derby CD (2008) Spiny lobsters detect conspecific blood-borne alarm cues exclusively through olfactory sensilla. *J Exp Biol* 211:2600–2608
- Sih A (1985) Evolution, predator avoidance, and unsuccessful predation. *Am Nat* 125:153–157
- Sih A (1987) Predators and prey lifestyles: an evolutionary and ecological overview. In: Kerfoot WC, Sih A (eds) *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, NH, p 203–244
- Smale M (1974) The warning squeak of the Natal rock lobster. *S Afr Assoc Mar Biol Res Bull* 11:17–19
- Smith RJF (1986) Evolution of alarm signals: role of benefits of retaining group members or territorial neighbors. *Am Nat* 128:604–610
- Spanier E, Weihs D, Galit AS (1991) Swimming of the Mediterranean slipper lobster. *J Exp Mar Biol Ecol* 145:15–31
- Vermeij GJ (1982) Unsuccessful predation and evolution. *Am Nat* 120:701–720
- Weiss HM, Lozano-Álvarez E, Briones-Fourzán P, Negrete-Soto F (2006) Using red light with fixed-site video cameras to study the behavior of the spiny lobster, *Panulirus argus*, and associated animals at night and inside their shelters. *Mar Technol Soc J* 40:86–95
- Weiss HM, Lozano-Alvares E, Briones-Fourzán P (2008) Circadian shelter occupancy patterns and predator-prey interaction of juveniles Caribbean spiny lobsters in a reef lagoon. *Mar Biol* 153:953–963
- Zhou S, Shirley TC (1997) Behavioural responses of red king crab to crab pots. *Fish Res* 30:177–189

Editorial responsibility: James McClintock,
Birmingham, Alabama, USA

Submitted: June 21, 2010; Accepted: November 22, 2010
Proofs received from author(s): February 4, 2011