Fishing gear modifications to reduce elasmobranch mortality in pelagic and bottom longline fisheries off Northeast Brazil

André S. Afonso a,b,*, Fábio H.V. Hazina a,1, Felipe Carvalhoc, José C. Pacheco f,1, Humberto Hazina a,1, David W. Kerstettere, Debra Muriec, George H. Burgessd

a Laboratório de Oceanografia Pesqueira, Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco, Rua Dom Manuel de Medeiros s/n, Dois Irmãos, CEP 52171-900, Recife/PE, Brazil
b Centro de Ciências do Mar do Algarve, Faculdade de Ciências do Mar e do Ambiente, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal
c Program of Fisheries and Aquatic Sciences, School of Forest Resource and Conservation, University of Florida, 7922 NW 71st St., Gainesville, FL 32653, USA
d Florida Program for Shark Research, Florida Museum of Natural History, University of Florida (UF P.O. Box 117800), Museum Road, Gainesville, FL 32611-7800, USA
e Nova Southeastern University Oceanographic Center, 8000 North Ocean Drive, Dania Beach, FL 33004, USA
f Program of Fisheries and Aquatic Sciences, School of Forest Resource and Conservation, University of Florida, 7922 NW 71st St., Gainesville, FL 32653, USA

* Corresponding author at: Laboratório de Oceanografia Pesqueira, Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco, Rua Dom Manuel de Medeiros s/n, Dois Irmãos, CEP 52171-900, Recife/PE, Brazil.
Tel.: +55 81 3320 6500; fax: +55 81 3320 6512.
E-mail address: afonso.andre@gmail.com (A.S. Afonso).

1 Tel.: +55 81 3320 6500; fax: +55 81 3320 6512.

© 2011 Elsevier B.V. All rights reserved.

A R T I C L E   I N F O
Article history:
Received 24 July 2010
Received in revised form 28 December 2010
Accepted 11 January 2011

Keywords:
Bycatch
Circle hook
Fishing mortality
MPUE
Shark
Selectivity

A B S T R A C T
One of the biggest challenges of fisheries research is reducing the bycatch of unwanted species. The incidental fishing mortality of species with low reproductive rates, such as elasmobranchs (sharks, skates, and rays), is recognized as a key threat for their populations. In the present study, gear modifications related to the type of hook and position of the hook in the water column were tested to examine their effects on catch rates and mortality of elasmobranch species in both pelagic and coastal environments. Comparisons between circle (size 18/0, 0° offset) and J-style (size 9/0, 10° offset) hooks demonstrated that the circle hooks have a greater efficiency in reducing the mortality of most species caught, both in pelagic and coastal longline fisheries. Internal lodging of the hook was significantly less frequent for the individuals caught with circle hooks, which likely contributed to their higher survival rate at haulback. Additionally, circle hooks also increased the CPUE of elasmobranchs caught in the pelagic longline fishery, which was particularly evident for Carcharhinus falciformis and Prionace glauca. The position of the hook in the water column exhibited a strong influence on the species caught in the coastal bottom longline fishery. Suspending hooks in the middle of the water column reduced the bycatch of common demersal species, such as Carcharhinus acronotus, Ginglymostoma cirratum, and Dasyatis americana, while increasing the CPUE of potentially aggressive species, such as Galeocerdo cuvier and Carcharhinus leucas. The interaction of the type of hook utilized with its position in the water column appears to be an essential factor in the optimization of longline selectivity and minimization of bycatch mortality.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Many types of fishing activities have a significant effect on non-target populations, habitats, and communities (Hall, 1996; Kaiser et al., 2002; Pauly et al., 2001; Sainsbury, 1987). Incidental mortality of cetaceans, seabirds, sea turtles, sharks, rays, and teleosts in longline fisheries is recognized as a key threat for many of these species (Musick, 1999). Elasmobranch fishes, the sharks, skates, and rays, are generally top-level predators in most marine ecosystems (Cortés, 1999; Garcia and Majkowski, 1990; Lewison et al., 2004; Megalofonou et al., 2005). Their abundance is relatively small compared to groups situated in lower trophic levels. However, their life history parameters such as being long-lived, with delayed maturity and low reproductive rates, make them particularly sensitive to increased mortality above natural levels (Musick, 1999).

Over the past decade, there has been a global concern regarding the bycatch of elasmobranchs in fishing operations (e.g., Coelho et al., 2003; Megalofonou et al., 2005). The historically low economic value of shark, skate, and ray products compared to high value teleost fishes has resulted in a generally lower priority for research and conservation of elasmobranchs (Barker and Schluessel, 2005). However, in more recent years there has been an elevated demand for shark fins (Musick et al., 2000), which has significantly increased their economic value and simultaneously driven a growing global concern about shark conservation and management.

Cortés, 1999; Garcia and Majkowski, 1990; Lewison et al., 2004; Megalofonou et al., 2005). Their abundance is relatively small compared to groups situated in lower trophic levels. However, their life history parameters such as being long-lived, with delayed maturity and low reproductive rates, make them particularly sensitive to increased mortality above natural levels (Musick, 1999).

Over the past decade, there has been a global concern regarding the bycatch of elasmobranchs in fishing operations (e.g., Coelho et al., 2003; Megalofonou et al., 2005). The historically low economic value of shark, skate, and ray products compared to high value teleost fishes has resulted in a generally lower priority for research and conservation of elasmobranchs (Barker and Schluessel, 2005). However, in more recent years there has been an elevated demand for shark fins (Musick et al., 2000), which has significantly increased their economic value and simultaneously driven a growing global concern about shark conservation and management.

Cortés, 1999; Garcia and Majkowski, 1990; Lewison et al., 2004; Megalofonou et al., 2005). Their abundance is relatively small compared to groups situated in lower trophic levels. However, their life history parameters such as being long-lived, with delayed maturity and low reproductive rates, make them particularly sensitive to increased mortality above natural levels (Musick, 1999).

Over the past decade, there has been a global concern regarding the bycatch of elasmobranchs in fishing operations (e.g., Coelho et al., 2003; Megalofonou et al., 2005). The historically low economic value of shark, skate, and ray products compared to high value teleost fishes has resulted in a generally lower priority for research and conservation of elasmobranchs (Barker and Schluessel, 2005). However, in more recent years there has been an elevated demand for shark fins (Musick et al., 2000), which has significantly increased their economic value and simultaneously driven a growing global concern about shark conservation and management.
Although pelagic elasmobranchs are caught with a variety of fishing gears in the Atlantic Ocean, longline fisheries targeting tunas and swordfish account for the majority of catches (Anonymous, 2007). In Brazil, the pelagic longlining for tunas was started more than 50 years ago, in the northeastern region (Paiva and Le Gall, 1975), with sharks always representing an important part of the bycatch (Hazin et al., 1998). In the tuna fleet operating in the south of Brazil, the landings of sharks have also been historically important, increasing throughout time, while the catch of tuna tended to decline (Anuska-Pereira et al., 2005). Regarding longline fisheries on coastal environments, there is little activity in Brazilian waters except for a long term, research monitoring program that has been surveying potentially aggressive sharks using bottom longlines in a region with an abnormally high shark attack rate (see Hazin et al., 2008). Within the scope of this research survey, target species correspond to potentially aggressive sharks (mostly large carcharhinids), while all the remaining, inoffensive taxa are interpreted as bycatch.

Concerns regarding the impact of fisheries on shark populations have led the United Nations’ Food and Agriculture Organization (FAO) to adopt the International Plan of Action for the Conservation and Management of Sharks (FAO, 1999). Both global and regional frameworks have also been constructed to solve issues related to the incidental catch of sharks for stock management purposes. However, management tools such as quotas and prohibited species are based on the assumption that individuals of regulated species are returned to the sea alive, which could be erroneous in case such species exhibit high at-vessel fishing mortality (Morgan and Burgess, 2007). To be effective, conservation measures need to be accompanied by complimentary tools that promote the meeting of their assumptions. In that respect, gear modifications are expected to be one of the most effective and inexpensive tools in reducing incidental fishing mortality (Brewer et al., 1996; Fonteyne and M’Rabet, 1992; Madsen et al., 2006).

Modifications to pelagic longline gear have often included changes in terminal tackle from J-style hooks to circle hooks. Circle hooks are distinct because their point is aligned perpendicular to their shank rather than parallel to it, as it is commonly the case with traditional hook types such as the J-style hook (Cooke and Suski, 2004). Due to their design, circle hooks tend to minimize deep hooking in potentially lethal internal regions and instead typically hook fish in the upper jaw (Montrey, 1999). Also, the catch rate of target species appears not to be significantly affected by the use of circle hooks in the case of tuna and billfishes, and it has been reported to even increase in comparison with J-style hooks, in some cases (Kerstetter et al., 2007; Falterman and Graves, 2002; Kerstetter and Graves, 2006; but see Read, 2007). Because of its performance, fishery managers have focused considerable attention on circle hooks as a way to reduce bycatch. This type of hook is currently being tested in different types of fisheries and has been shown to be a practical and economical measure of hook is currently being tested in different types of fisheries and has been shown to be a practical and economical measure to reduce mortality in pelagic longline fisheries. Despite previous studies on the mortality rate (Falterman and Graves, 2002), catch rate (Prince et al., 2002), hooking efficiency (Skomal et al., 2002), and hook location on teleost fishes (Bachelier and Buckel, 2004; Beckwith and Rand, 2005), there is little published information on the influence of hook type in the catches and mortality of elasmobranchs, with a few exceptions (e.g., Kerstetter and Graves, 2006). In the South Atlantic fisheries, such information is nonexistent.

The vertical position of the hooks across the gear (Fig. 2). The gear configuration used for these sets was similar to that traditionally used by the pelagic longline fishery off Northeast Brazil, which targets tuna with a 3.5 mm monofilament mainline, 18 m buoy floats, and 18 m branch lines with 3.6 m monofilament leaders. Bait was composed of skipjack (Katsuwonus pelamis).

Fig. 1. Study area. Location of the 12 longline sets (black circles) of the pelagic experiment in the Equatorial Atlantic Ocean, and of the coastal longline sets (black rectangles) conducted off the metropolitan region of Recife.
Fig. 2. Pelagic longline. Schematic drawing of the gear used in the pelagic bycatch experiment to compare the performance of circle and traditional J-style hooks by alternating them throughout the set.

Species composition, catch rate, and condition of caught individuals (alive or dead) at the time of haulback were recorded in relation to hook type. Although the sets encompassed only 650 hooks, catch rates were expressed as catch-per-unit-effort (CPUE) in number of individuals caught per 1000 hooks to preserve clarity. Hooking location was also recorded for each fish caught during the pelagic experiment, following Kerstetter and Graves (2006), and were characterized into three types: (1) “external”, if the hook lodged in the edge of the jaw, the corner of the mouth, or the snout/bill area; (2) “internal”, if the hook was swallowed (non-visible) or lodged in the roof of the mouth or throat; and (3) “entangled”, if the fish was entangled in the leader or hooked on the body other than mouth region.

2.2. Bottom longlining experiment

In the second experiment, 608 bottom longline research sets were monitored off the coast of Recife, Northeast Brazil, within the scope of a shark monitoring program that targeted potentially aggressive carcharhinids because of an abnormally high incidence of shark attacks on humans in the area (see Hazin et al., 2008). Fishing was conducted in a 20 km nearshore area stretching between Pina and Paiva Beaches (Fig. 1), which included the Barra das Jangadas estuarine system. Fishing gear was set at depths ranging between 8 and 14 m, corresponding to a distance of about 1–3 km from the coastline. The bottom longline consisted of one main 8 mm multifilament polyamide line 4 km in length, subdivided into four sections with 25 hooks each, thus totaling 100 hooks per set. The branch lines were composed of an 8 m long monofilament line that was 3.0 mm in diameter, which was followed by a stainless steel leader of 2 m (Fig. 3). Bait was composed of moray-eel (Gymnothorax sp.). This experiment was conducted in two distinct phases. During the first phase, spanning from September 2004 to August 2005, 384 sets were conducted using only J-style hooks. During this phase, the influence of the vertical position of the hook on the catch composition and catch rate of elasmobranchs was determined by deploying half of the hooks demersally (i.e., sitting on the bottom), while suspending the other half in mid-water by attaching one 200 cm³, cylindrical Styrofoam buoy (almost 200 g flotation; P.G. Albuquerque, UFRPE, pers. comm.) to the proximal end of the leader of each secondary line with a snap, about 2 m from the hook. The latter configuration assured that hooks would fish in the upper half of the water column independently of tidal height or current speed. In the second phase, extending from May 2006 to April 2007, the influence of hook type on catch rate and mortality at haulback was compared during 224 sets by alternating circle and J-style hooks along a mainline with all hooks suspended in mid-water (Fig. 3). Both circle and J-style hooks used in the bottom longlining experiment were identical to the hooks used in the pelagic longlining experiment (Section 2.1).

Data on species composition, CPUE, and condition of caught individuals (alive or dead) at the time of haulback were recorded in relation to fishing depth of the hook (phase 1) and hook type (phase 2) during the bottom longline experiment. CPUE was expressed as
Fig. 3. Demersal longline. Schematic drawing of the coastal longline used off Recife, Brazil; bottom: first phase, using only J-style hooks either suspended in the water column or laying on the bottom; middle: details of the branch lines utilized in both phases; top: second phase, using alternating J-style and circle hooks both suspended in the water column.

number of individuals caught per 1000 hooks to allow for comparisons. For both experiments, CPUE of dead specimens, hereafter referred to as mortality-per-unit-effort (MPUE), was calculated for all elasmobranch species as a way to combine the catch rate with the at-vessel mortality rate. Fish that did not actively move in the water or on deck were conservatively considered “dead”. Differences in CPUE between circle hooks and J-style hooks and between hooks suspending in the water column and hooks deployed on the sea floor were tested for species with >10 individuals caught. Paired t-tests were conducted after assessing homoscedasticity with a Levene’s test and performing the \( X = \log(X + 1) \) transformation to conform to the assumption of normality (Zar, 1996). As in Kerstetter and Graves (2006), the Cochran–Mantel–Haenszel chi-square test (CMH \( X^2 \)) was used to compare species differences in mortality at haulback and differences in hooking location between the two hook types, since the robustness of the test allows relatively low sample sizes. SAS/STAT (SAS Institute Inc., 2006) was used for all statistical analyses.

3. Results

3.1. Pelagic longlining experiment

Overall, the pelagic longline sets (7800 hooks) caught 134 sharks corresponding to 10 species (Table 1). The night shark, *Carcharhinus signatus*, and the blue shark, *Prionace glauca*, were the most common shark species caught, comprising 48.5% of the total shark bycatch, followed by the silky shark, *C. falciformis* (10.4%), the oceanic whitetip, *C. longimanus* (9.0%), the scalloped hammerhead, *Sphyrna lewini* (8.2%), the dusky shark, *Carcharhinus obscurus* (7.4%), the tiger shark, *Galeocerdo cuvier* (6.0%), the nurse shark, *Ginglymostoma cirratum* and the shortfin mako, *Isurus*
Elasmobranch mortality rate at haulback varied considerably among species and hook types (Table 1). The night shark had 100% relative mortality on both hook types, in contrast to the blue (CMH = 0.731). CPUE for the night (t = 4.011, P < 0.002), silky (CMH = 0.006), and oceanic whitetip (t = 1.249, P = 0.031) sharks were significantly greater with circle hooks as opposed to J-style hooks. Despite low overall catch (≤10 individuals), dusky, tiger, shortfin mako, and nurse sharks also tended to be caught more with circle hooks than J-style hooks (Table 1).

Elasmobranch mortality rate at haulback varied considerably among species and hook types (Table 1). The night shark had 100% relative mortality on both hook types, in contrast to the nurse shark that had 0% mortality on both types of hook. The blue (CMH = 2.31, P = 0.002), silky (CMH = 1.79, P = 0.006), and oceanic whitetip (CMH = 1.003, P = 0.002) sharks had significantly higher relative mortality at haulback with J-style hooks than with circle hooks, with scalloped hammerhead, dusky, tiger, shortfin mako, and bull sharks following this trend but not tested statistically due to small sample sizes. In spite of both types of hook presenting equal relative fishing mortality for the night shark, the associated MPUE was considerably higher with circle hooks, due to the higher CPUE of this species with this hook type. In contrast, the MPUE of J-style hooks was higher for blue, silky, scalloped hammerhead, dusky, and oceanic whitetip (CMH = 0.031) sharks.

3.2. Bottom longlining experiment

During the first phase of the research using bottom longline to test for the influence of fishing depth on CPUE, 109 elasmobranchs were caught on a total of 11,200 hooks, including 46 rays and 63 sharks represented by nine species (Table 2). Demersal hooks showed significantly higher CPUE than hooks suspended in the water column for blacknose (t = 2.341, P = 0.002) and nurse (t = 3.001, P < 0.001) sharks, as well as for southern stingray (t = 1.038, P = 0.013). Levene’s test showed no significant differences between CPUE variances of hooks suspending in the water column and hooks deployed on the sea floor (F = 1.778, P = 0.207). Sharks also tended to be caught more with circle hooks than J-style hooks (Table 2).

Species considered potentially aggressive, including the tiger, the bull, the blacktip, and the scalloped hammerhead sharks (ISAF, 2008), were caught infrequently but always on the suspended hooks (Table 2).
significantly higher using circle hooks (Fig. 5). Since both hook types are known to reduce the rate of deep hooking and to increase mouth leaders and thus escape detection. The use of circle hooks has been shown to be effective in reducing shark mortality (Gilman et al., 2008).

In the second phase of the bottom longlining experiment comparing hook types, 38 specimens were caught on a total of 11,097 hooks. Comparison between circle and J-style hooks showed no significant differences in CPUE for the species analyzed. Levene’s test found no significant differences between CPUE variances of both types of hook (F = 3.87, P = 0.347). Southern stingray, nurse shark, and manta ray suffered no mortality from either hook type. The number of tiger (CMH^2 = 4.330, P < 0.001) and blacknose (CMH^2 = 2.221, P < 0.001) sharks alive at haulback, however, was significantly higher using circle hooks (Fig. 5). Since both hook types showed similar catch rates, circle hooks could be misleading because sharks that were gut-hooked by J-style hooks were more likely to bite off monofilament leaders and thus escape detection. The use of circle hooks has been known to reduce the rate of deep hooking and to increase mouth hooking in some pelagic fish such as the Atlantic bluefin tuna, Thunnus thynnus, yellowfin tuna, T. albacares, and Istiophorid billfishes (e.g., Falterman and Graves, 2002; Prince et al., 2002; Skomal et al., 2002; Kerstetter and Graves, 2006). The present study follows the assumption that the difference in the catch rate between circle and J-style hooks only results from an interaction after the shark biting the bait, i.e., different hooks will not exhibit different attractiveness or elicit distinct behaviors and catch differences are only ascribed to distinct gear capacities to hook and to retain the animal until retrieval of the gear. Therefore, the significantly higher catch rates found for circle hooks could only be attributed either to a lower probability of a shark to avoid being hooked after biting the bait or to escape the hook after being caught. Unfortunately, the absence of hooks in the secondary lines was not tracked at haul-back, making it impossible to investigate these possibilities. We therefore encourage future hook type comparison experiments to include missing hooks (i.e., so-called “bite-offs”) at gear retrieval within their data collection protocols.

The type of hook in the bottom longline experiment did not present any significant effect on the catch rates of elasmobranchs, a pattern that might be related to the fact that stainless steel leaders were used in this fishing gear, thus reducing the probability of sharks escaping after biting off the monofilaments in the case of deep hooking (Gilman et al., 2008).

In the pelagic longline sets, the circle hooks showed significantly lower mortality rates at haulback for three of the species caught, most likely due to the lower rate of internal hooking. This is consistent with the findings of prior studies in teleosts (Domier et al., 2003; Horodysky and Graves, 2005), yet Yokota et al. (2006) found no significant differences in the blue shark mortality rate using tuna hooks and two sizes of circle hooks. In the present study, the mortality per unit of effort (MPUE) was calculated in order to compare fishing impacts of both hooks used. Circle hooks resulted in a higher MPUE of C. signatus, but only due to its higher CPUE with this hook type, since in both hooks all specimens of this species were dead at haulback. Such severe mortality could be associated to a particularly low resilience of this species. The MPUE for five other species, however, was considerably lower with the circle hooks, in spite of a generally higher CPUE. Besides, if the absence of stainless steel leaders indeed influenced the CPUE of specimens caught with J-style hooks, a significant portion of the individuals that escaped detection might have not survived due to the injuries inflicted by the fishing gear, and this ultimately may have resulted in an underestimation of the mortality induced by J-style hooks. Further studies will be required to analyze the effect of the interactions between leader materials and hook type on shark CPUE and mortality before reaching any definitive conclusion.

In the present study, circle hooks decreased relative mortality at haulback of most species caught. Externally hooked individuals most likely have higher survival rates, and therefore such animals are expected to die not from direct injuries inflicted by the fishing gear but presumably from the physiological stress caused by the capture and, in some species, from insufficient oxygenation caused by swimming constraints (Brill et al., 2008; Manire et al., 2001; Skomal, 2007; Young et al., 2002). This was corroborated to some extent by MPUE results, which provided potentially useful information for management purposes, like the eventual adoption of a mandatory release of alive elasmobranchs, which has precedence for other species in Brazilian waters (e.g. both white and blue marlins alive at haul-back are currently required to be released). Thus, at least for some species of sharks, the fishing mortality of externally hooked individuals appears to be ultimately shaped by gear soak time. Conservation measures aiming to reduce bycatch post-release mortality by requiring the reduction of soak time coupled with the mandatory release of sharks and rays that are alive at the time of haulback could, therefore, be much more effective with the use of circle hooks.

The shark and ray species caught using bottom longline in the coastal sets off Pernambuco are the same species as those identified in previous surveys in that area. This included potentially aggressive species recognized as being involved in shark attack incidents in the beaches of Pernambuco, such as tiger and bull sharks (Hazin et al., 2000), and several other rather inoffensive species, such as the southern stingray, and the blacknose and nurse sharks. The high relative abundances of the three latter species could be attributed to their distribution, since they are known to typically inhabit shallow, nearshore areas of the continental shelf in the western Atlantic Ocean (Bigelow and Schroeder, 1948).

The influence of the vertical position of the hook on catch rates is probably a consequence of the feeding depth distribution of the species caught, as previously proposed by other authors. Bigelow and Schroeder (1948) and Compagno (2002) described the blac-
knob and nurse sharks, as well as the southern stingray, as species highly associated with demersal habitats, whereas the tiger, bull, and blacktip sharks and scalloped hammerhead would more commonly swim and feed in the middle depths of the water column. The suspension of the hooks in midwater depths, therefore, significantly increased the selectivity of the longline by sharply reducing the catch rates of demersal species, such as blacknose and nurse sharks and the southern stingray, while increasing the CPUE of species that swim in the water column, such as the tiger and bull sharks. Similarly to the pelagic longline, the use of circle hooks in the bottom longline also significantly decreased the mortality rate at haulback of two of the species caught, thereby increasing the number of successful post-capture releases.

Overall, the present results indicate that rather simple, non-expensive gear modifications, such as changing the type of hook and the relative hook position within the water column, may be an efficient way to increase longline selectivity and to reduce bycatch, while decreasing significantly the fishing mortality of unwanted species. While there could be a concern regarding the impact of such modifications on the catch rate of valuable target species, such as tunas and billfishes, growing evidence has been demonstrating that some strategies have no negative effects on harvest, and so they would not necessarily pose any economical threat to fisheries. In spite of the catch rate of tunas and billfishes was not herein addressed, a recent study conducted in the same region verified that the circle hook utilized in this experiment did not exhibit any reduction in the CPUE of that target group when compared to the commonly used J-style hook (Pacheco et al., 2011). Thus, it seems advisable to consider such potentially effective measures for integrating more efficient management plans of oceanic fisheries, especially given the fact that they are comparably inexpensive and quick to implement.

Role of the funding source

None of the funding institutions had any further involvement on the present study.

Acknowledgements

This study was funded by the Financiadora para Estudos e Projetos do Ministério da Ciência, Tecnologia e Inovação (FINEP/MCT), Ministry of Fisheries and Aquaculture, the State Government of Pernambuco, the City Hall of Recife, and the Fundação para a Ciência e Tecnologia (Portugal). We are also grateful to the Tropical Conservation and Development Program (TCD), the Program of Fisheries and Aquatic Science, and Florida Program for Shark Research at the University of Florida- USA, for the Fellowship/Assistantship provided to Felipe Carvalho. The authors would like to acknowledge the Instituto Oceanário de Pernambuco, NOAA/NMFS (for providing all circle hooks used in the experiment), Norpeixe (for allowing the experiments to be conducted aboard one of their vessels), the Captain and crew of F/V Alf a and R/V Sinu elo for assisting with field work, and two anonymous reviewers for their precious suggestions.

References