

Figure 4. Relationship between nest stone area (cm²) and the number of eggs in the nests (N eggs) for A) *Padogobius nigricans* (N = 98) and B) *P. bonelli* (N = 157) in stations of the upper River Tiber.

shelter could potentially be a limiting resource, making any competition between the two gobies much stronger (Błońska et al. 2016). If shelters are limited, it's likely that the more aggressive *P. bonelli* is a stronger competitor, ultimately excluding *P. nigricans* from the reproductive habitat. In laboratory conditions, *P. bonelli* males directly compete with conspecifics for possession of larger nest sites, because females use nest size as a predictor of male quality (Lindström 1988; Bisazza et al. 1989). The nest is a substrate which may physically limit the size of eggs mass in these species that lay eggs in a single layer, and thus, the ability of a male to spawn clutches (Lindström 1988; Marconato et al. 1989). For both species, as in most gobiids (Lindström 1988; Marconato et al. 1989; Takahashi et al. 2001), the number of the eggs in the clutches depends on the lower surface area of the nest, thus it is likely that males compete for larger stones which allow them to mate with more than one female, thereby maximizing reproductive success (Marconato et al. 1989). Moreover, in fish species with exclusive paternal care, females usually favour large nests (Takahashi and Khoda 2002). They prefer to spawn with males whose nests already contain eggs (Forsgren et al. 1996) and large brood sizes may induce more paternal care (Coleman et al. 1985). The preliminary results of this study indicate that *P. nigricans* occupied on average the larger nests and produced more eggs per nest. Moreover, no differences were found in nest characteristics (size and number of eggs) of *P. nigricans* between the

invaded and uninvaded areas. Thus *P. bonelli* seems to interfere not with the “quality” of *P. nigricans* nests, but rather with the “quantity”. Moreover, shelter is not only an essential environmental resource during the spawning period for both species, it also plays significant roles in predator protection and refuge from stream flows (Allouche 2002).

Occupying the best sites is apparently not enough for the conservation of *P. nigricans*. In the invaded areas, the survival of *P. nigricans* populations is mostly through migration of individuals from uninvaded areas located upstream of weirs that prevented the spread of the non-native species. Passive movement of early ontogenetic stages may represent an important dispersal mechanism in gobies (Janáč et al. 2013). In this sense, small weirs have had a dual task: they facilitate the survival of intact populations of *P. nigricans*, and allow recolonization of invaded areas, preventing long-term inter-specific exclusion (Belkessam et al. 1997). River damming is one of the most damaging anthropogenic alterations for freshwater environments (Baxter 1977; Dynesius and Nilsson 1994; Franchi et al. 2014). Damming impedes free movement of fish, emphasizing the consequences of isolation (Lorenzoni et al. 2006). Nevertheless, the presence of such barriers substantially contributes to the preservation of isolated populations of vulnerable and endangered species; for this reason actions to restore connectivity between rivers must take into account the risk of spread of invasive species (Van Kessel et al. 2016).

Acknowledgements

We thank the administration Umbria Region that provided the permissions to carry out the field samplings. We are particularly grateful to F. Vercillo of Perugia University for its fundamental assistance in the development of PCR-RFLP protocol and G. La Porta of Perugia University for its advice on statistical analyses. We also thank C. Cauzillo for field work and I. Şener of Muğla University for assistance in the laboratory. We are extremely grateful to the reviewers for their constructive comments that have significantly improved the manuscript and to the Editors for their valuable effort in the pre-evaluation and revision processes of the manuscript.

References

- Allouche S (2002) Nature and functions of cover for riverine fish. *Bulletin Francais de la Peche et de la Pisciculture* 365/366: 297–324, <https://doi.org/10.1051/kmae:2002037>
- Bagenal TB, Tesch FW (1985) Age and growth. In: Bagenal TB (ed), Fish production in freshwaters. Blackwell, London, pp 101–136
- Baxter RM (1977) Environmental effects of dams and impoundments. *Annual Review of Ecology, Evolution and Systematics* 8: 255–283, <https://doi.org/10.1146/annurev.es.08.110177.001351>
- Belkessam D, Oberdorff T, Huguency B (1997) Unsaturated fish assemblages in rivers of north-western France: potential consequences for species introductions. *Bulletin Francais de la Peche et de la Pisciculture* 344–345: 193–204, <https://doi.org/10.1051/kmae:1997022>
- Bergstrom MA, Evrard LM, Mensinger AF (2008) Distribution, abundance, and range of the Round Goby, *Apollina melanostoma*, in the Duluth-Superior Harbor and St Louis River Estuary, 1998–2004. *Journal of Great Lakes Research* 34: 535–543, [https://doi.org/10.3394/0380-1330\(2008\)34\[535:DAAROT\]2.0.CO;2](https://doi.org/10.3394/0380-1330(2008)34[535:DAAROT]2.0.CO;2)
- Bianco PG (1995) Mediterranean endemic freshwater fishes of Italy. *Biological Conservation* 72: 159–170, [https://doi.org/10.1016/0006-3207\(94\)00078-5](https://doi.org/10.1016/0006-3207(94)00078-5)
- Bianco PG, Ketmaier V (2001) Anthropogenic changes in the freshwater fish fauna of Italy, with reference to the central region and *Barbus graellsii*, a newly established alien species of Iberian origin. *Journal of Fish Biology* 59: 190–208, <https://doi.org/10.1111/j.1095-8649.2001.tb01386.x>
- Bisazza A, Marconato A, Marin G (1989) Male competition and female choice in *Padogobius martensi* (Pisces, Gobiidae). *Animal Behaviour* 38: 406–413, [https://doi.org/10.1016/S0003-3472\(89\)80033-8](https://doi.org/10.1016/S0003-3472(89)80033-8)
- Błońska D, Kobak J, Kakareko T, Grabowska J (2016) Can the presence of alien Ponto-Caspian gobies affect shelter use by the native European bullhead? *Aquatic Ecology* 50: 653–665, <https://doi.org/10.1007/s10452-016-9584-1>
- Brownscombe JW, Fox MG (2012) Range expansion dynamics of the invasive round goby (*Neogobius melanostomus*) in a river system. *Aquatic Ecology* 46: 175–189, <https://doi.org/10.1007/s10452-012-9390-3>
- Coleman RM, Gross MR, Sargent RC (1985) Parental investment decision rules: a test in the bluegill sunfish. *Behavioral Ecology and Sociobiology* 18: 59–66
- Crivelli AJ (2006) *Padogobius nigricans* In: IUCN Red List of Threatened Species. <http://dxdoiorg/102305/IUCNUK2006RLTST15870A5263874en> (accessed 16 January 2017).
- Dynesius M, Nilsson C (1994) Fragmentation and flow regulation of river systems in northern third of the world. *Science* 266: 753–762, <https://doi.org/10.1126/science.266.5186.753>
- Forsgren E, Karlsson A, Kvamemo C (1996) Female sand gobies gain direct benefits by choosing males with eggs in their nests. *Behavioral Ecology and Sociobiology* 39: 91–96, <https://doi.org/10.1007/s002650050270>
- Franchi E, Carosi A, Ghetti L, Giannetto D, Pedicillo G, Pompei L, Lorenzoni M (2014) Changes in the fish community of the upper Tiber River after construction of a hydro-dam. *Journal of Limnology* 73: 1–8, <https://doi.org/10.4081/jlimnol.2014.876>
- Giannetto D, Carosi A, Franchi E, Ghetti L, Pedicillo G, Pompei L, Lorenzoni M (2012) Assessing the impact of non-native freshwater fishes on native species using relative weight. *Knowledge and Management of Aquatic Ecosystems* 404: 03, <https://doi.org/10.1051/kmae/2011081>
- Grabowska J, Kakareko T, Błońska D, Przybylski M, Kobak J, Jermacz Ł, Copp GH (2016) Interspecific competition for a shelter between non-native racer goby and native European bullhead under experimental conditions - Effects of season, fish size and light conditions. *Limnologica* 56: 30–38, <https://doi.org/10.1016/j.limno.2015.11.004>
- Gutowksy LFG, Brownscombe JW, Fox MG (2011) Angling to estimate the density of large round goby (*Neogobius melanostomus*). *Fisheries Research* 108: 228–231, <https://doi.org/10.1016/j.fishres.2010.12.014>
- Hayden TA, Miner JG (2009) Rapid dispersal and establishment of a benthic Ponto-Caspian goby in Lake Erie: Diel vertical migration of early juvenile round goby. *Biological Invasions* 11: 1767–1776, <https://doi.org/10.1007/s10530-008-9356-5>
- Irons KS, McClelland MA, Pegg MA (2006) Expansion of round goby in the Illinois Waterway. *The American Midland Naturalist* 156: 198–200, [https://doi.org/10.1674/0003-0031\(2006\)156\[198:EORG IT\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2006)156[198:EORG IT]2.0.CO;2)
- Janáč M, Šlapanský L, Valová Z, Jurajda P (2013) Downstream drift of round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*) in their non-native area. *Ecology of Freshwater Fish* 22: 430–438, <https://doi.org/10.1111/eff.12037>
- Janssen J, Jude DJ (2001) Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *Journal of Great Lakes Research* 27: 319–328, [https://doi.org/10.1016/S0380-1330\(01\)70647-8](https://doi.org/10.1016/S0380-1330(01)70647-8)
- Jermacz Ł, Kobak J, Dzierżyńska A, Kakareko T (2014) The effect of flow on the competition between the alien racer goby and native European bullhead. *Ecology of Freshwater Fish* 24: 467–477, <https://doi.org/10.1111/eff.12162>
- Kakareko T, Kobak J, Grabowska J, Jermacz Ł, Przybylski M, Poznańska M, Pietraszewski D, Copp GH (2013) Competitive interactions for food resources between invasive racer goby *Bakka gymnotrachelus* and native European bullhead *Cottus gobio*. *Biological Invasions* 15: 2519–2530, <https://doi.org/10.1007/s10530-013-0470-7>
- Kottelat M, Freyhof J (2007) Handbook of European freshwater fishes. Kottelat, Cornol, Switzerland, 646 pp
- Lindström K (1988) Male-male competition for nest sites in the sand goby, *Pomatoschistus minutus*. *Oikos* 53: 67–73, <https://doi.org/10.2307/3565664>
- Lorenzoni M, Carosi A, Ghetti L, Dolciami R (2010) La fauna ittica e i corsi d'acqua dell'Umbria Sintesi delle carte Ittiche regionali dal 1986 al 2009. Regione Umbria, Italy, 287 pp
- Lorenzoni M, Ghetti L, Mearrelli M (2006) Native and exotic fish species in the Tiber River watershed (Umbria - Italy) and their relationship to the longitudinal gradient. *Bulletin Francais de la Peche et de la Pisciculture* 382: 19–44, <https://doi.org/10.1051/kmae:2006005>
- Lorenzoni M, La Porta G, Pedicillo G, Spigonardi MP, Carosi A, Vitali P, Baldini G, Ghetti L, Zeetti A, Natali M, Biscaro Parrini A, Dolciami R, Mezzetti A, Burchia A, Di Brizio M, Pancioni T, Uzzoli C (2007) Carta Ittica della Regione Umbria: bacino del Fiume Tevere. Regione dell'Umbria, Perugia, Italy, 305 pp
- Lugli M, Bobbio L, Torricelli P, Gandolfi G (1990) Analisi dei fattori che influenzano la distribuzione nello spazio dei riproduttori di *Padogobius martensi* (Pisces, Gobiidae). *Rivista di Idrobiologia* 29: 300–308
- Marconato A, Bisazza A, Marin G (1989) Correlates of male reproductive success in *Padogobius martensi* (Gobiidae). *Journal of Fish Biology* 34: 889–899, <https://doi.org/10.1111/j.1095-8649.1989.tb03372.x>
- Mearrelli M, Lorenzoni M, Carosi A, Giovinnazzo G, Petesse ML (1996) Carta Ittica della Regione Umbria Regione Umbria, Perugia, Italy

- Mecatti M, Gualtieri M, Gattai K (2010) Transfaunazioni invasive nel distretto ittiofaunistico tosco-laziale: prove di competizione territoriale e alimentare tra *Padogobius nigricans* e *Padogobius bonelli*. *Studi Trentini di Scienze Naturali* 87: 133–136
- Miller PJ (1990) The endurance of endemism: the Mediterranean freshwater gobies and their prospects for survival. *Journal of Fish Biology* 37: 145–156, <https://doi.org/10.1111/j.1095-8649.1990.tb05030.x>
- Moran PAP (1951) A mathematical theory of animal trapping. *Biometrika* 38: 307–311, <https://doi.org/10.1093/biomet/38.3-4.307>
- Nocita A, Zerunian S (2007) L'ittiofauna aliena nei fiumi e nei laghi d'Italia. *Biologia Ambientale* 21: 93–96
- Pompei L, Giannetto D, Lorenzoni M (2014) Feeding ecology of *Padogobius nigricans* (Canestrini, 1867) and *P. bonelli* (Bonaparte, 1846) in Aggia River (Umbria, Italy) and their diet overlap. *Hydrobiologia* 740: 101–113, <https://doi.org/10.1007/s10750-014-1942-1>
- Pompei L, Giannetto D, Lorenzoni M (2016a) Reproductive parameters in native and non-native areas of *Padogobius bonelli* and comparison with *P. nigricans* (Actynopterygii, Gobiidae). *Hydrobiologia* 779: 173–182, <https://doi.org/10.1007/s10750-016-2812-9>
- Pompei L, Giannetto D, Lorenzoni M (2016b) The non-native goby *Padogobius bonelli* in the River Tiber, Italy and its effect on the reproductive potential of the native goby, *P. nigricans*. *Aquatic Invasions* 11: 83–92, <https://doi.org/10.3391/ai.2016.11.1.09>
- Raby G, Gutowsky L, Fox MG (2010) Diet composition and consumption rate in round goby (*Neogobius melanostomus*) in its expansion phase in the Trent River, Ontario. *Environmental Biology of Fish* 89: 143–150, <https://doi.org/10.1007/s10641-010-9705-y>
- Roche KF, Janač M, Jurajda P (2013) A review of Gobiid expansion along the Danube-Rhine corridor – geopolitical change as a driver for invasion. *Knowledge and Management of Aquatic Ecosystems* 411: 01, <https://doi.org/10.1051/kmae/2013066>
- Rondinini C, Battistoni A, Peronace V, Teofili C (2013) Lista Rossa IUCN dei Vertebrati Italiani. Comitato Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Roma, Italy, pp 56
- Steingraeber MT, Thiel PA (2000) The round goby (*Neogobius melanostomus*): another unwelcome invader in the Mississippi River Basin. In: McCabe RE, Loos SE (eds) (2000) Transactions of the 65th North American Wildlife and Natural Resources Conference. Wild life Management Institute, Washington DC, USA, pp 328–344
- Takahashi D, Kohda M (2002) Female preference for nest size in the Stream Goby *Rhinogobius* sp. DA. *Zoological Science* 19: 1241–1244, <https://doi.org/10.2108/zsj.19.1241>
- Takahashi D, Kohda M, Yanagisawa Y (2001) Male-male competition for large nests as a determinant of male mating success in a Japanese stream goby, *Rhinogobius* sp. DA. *Ichthyological Research* 48: 91–95, <https://doi.org/10.1007/s10228-001-8121-x>
- Torricelli P, Lugli M, Gandolfi G (1986) A quantitative analysis of the occurrence of visual and acoustic displays during the courtship in the freshwater goby, *Padogobius martensi* (Günther, 1961) (Pisces, Gobiidae). *Italian Journal of Zoology* 53: 85–89, <https://doi.org/10.1080/11250008609355488>
- Van Kessel N, Dorenbosch M, de Boer MRM, Leuven RSEW, Van Der Velde G (2011) Competition for shelter between four invasive gobiids and two native benthic fish species. *Current Zoology* 57: 844–851, <https://doi.org/10.1093/czoolo/57.6.844>
- Van Kessel N, Dorenbosch M, Kranenbarg J, Van Der Velde G (2016) Invasive Ponto-Caspian gobies rapidly reduce the abundance of protected native bullhead. *Aquatic Invasions* 11: 179–188, <https://doi.org/10.3391/ai.2016.11.2.07>
- Vercillo F, Lucentini L, Mucci N, Ragni B, Randi E, Panara F (2004) A simple and rapid PCR-RFLP method to distinguishing *Martes martes* and *Martes foina*. *Conservation Genetics* 5: 869–871, <https://doi.org/10.1007/s10592-004-1866-9>
- Zerunian S (2002) Condannati all'estinzione? Biodiversità, biologia, minacce e strategie di conservazione dei Pesci d'acqua dolce indigeni in Italia Edagricole, Bologna, Italy, 230 pp
- Zerunian S, D'Onofrio E, Gibertini G (1988) The biology of *Gobius nigricans* (Osteichthyes, Gobiidae) I Observations on the reproductive behaviour. *Bolletino di Zoologia* 55: 293–298, <https://doi.org/10.1080/11250008809386626>
- Zippin C (1958) The removal method of population estimation. *Journal of Wildlife Management* 22: 82–90, <https://doi.org/10.2307/3797301>

Supplementary material

The following supplementary material is available for this article:

Table S1. Occurrence of non-native *P. bonelli* and native *P. nigricans* (presence in the upper River Tiber observed in the period 2011–2015).

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Pompei_et_al_Table_S1.xlsx