STRUKTURA POPULACIJE DOBROGA DUPINA Tursiops truncatus (Montagu, 1821) U ISTOČNOM JADRANU

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DOKTORSKI RAD

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FACULTY OF SCIENCE

DEPARTMENT OF BIOLOGY

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BOTTLENOSE DOLPHIN *Tursiops truncatus* (Montagu, 1821) POPULATION STRUCTURE IN THE EASTERN ADRIATIC SEA

DOCTORAL THESIS

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Ovaj je doktorski rad izrađen u Plavom svijetu Institutu za istraživanje i zaštitu mora, pod vodstvom doc. dr. sc. Draška Holcera, u sklopu Sveučilišnog poslijediplomskog doktorskog studija Biologije pri Biološkom odsjeku Prirodoslovno-matematičkog fakulteta Sveučilišta u Zagrebu.

O mentoru

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Sveučilište u Zagrebu Doktorski rad
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Biološki odsjek

STRUKTURA POPULACIJE DOBROGA DUPINA *Tursiops truncatus* (Montagu, 1821) U ISTOČNOM JADRANU

Grgur Pleslić

Plavi svijet Institut za istraživanje i zaštitu mora

Dobri dupin (*Tursiops truncatus*) jedini je morski sisavac koji trajno naseljava cijelo Jadransko more. Dosadašnja istraživanja ukazuju da je populacija u Jadranu strukturirana u lokalne zajednice, no njihova prostorna i društvena struktura nije bila opisana. Ova disertacija kroz tri znanstvena rada na temelju podataka prikupljenih foto-identifikacijom opisuje prostornu i društvenu strukturu populacije dobrog dupina duž istočne obale Jadranskog mora, istražuje čimbenike koji utječu na prostornu i društvenu strukturu populacije i po prvi put opisuje demografske parametre lokalne zajednice dobrog dupina u području sjeverne Dalmacije. U području od Istre do akvatorija otoka Visa utvrđene su tri zajednice dobrog dupina. Spol, jačina društvenih veza, nautički promet i koćarenje utvrđeni su kao čimbenici koji utječu na društvenu strukturu i područja obitavanja jedinki. Akvatorij sjeverne Dalmacije naseljava relativno mala, ali stabilna zajednica dobrog dupina. Ukupni rezultati ove disertacije podupiru pretpostavku o meta-populaciji dobrog dupina i daju smjer za daljnja istraživanja radi boljeg poznavanja ove vrste u Jadranu.

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University of Zagreb Doctoral thesis
Faculty of Science
Department of Biology

BOTTLENOSE DOLPHIN *Tursiops truncatus* (Montagu, 1821) POPULATION STRUCTURE IN THE EASTERN ADRIATIC SEA

Grgur Pleslić

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The bottlenose dolphin (*Tursiops truncatus*) is the only marine mammal permanently inhabiting the whole Adriatic Sea. Previous studies suggest that the population is structured into local communities, but the social and spatial structure remained unknown. This dissertation is based on three publications that, based on photo-identification data, describe the social and spatial structure of the bottlenose dolphin population along the eastern Adriatic coast, determine factors influencing the social and spatial structure of the population, and, for the first time, describe the demographic parameters of a community inhabiting the waters of north Dalmatia. Three local communities have been determined in the area between the Istrian peninsula and the island of Vis. Gender, association strengths, leisure boat traffic and trawling are factors influencing the social structure and individuals' home ranges. The waters of north Dalmatia are inhabited by a relatively small, but stable bottlenose dolphin community. The summary results of this dissertation support the hypothesis of meta-population and provide guidelines for future research to better understand the status of this species in the Adriatic Sea.

(97 pages / 2 figures / 2 tables / 130 references / original in: Croatian)

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1. UVOD

1.1. Biologija dobrog dupina

Dobri dupin, *Tursiops truncatus* (Montagu, 1821), pripada redu kitova (Cetacea) i podredu kitova zubana (Odontoceti). Kod roda *Tursiops*, razlike u veličini tijela, pigmentaciji te građi lubanje u ovisnosti o hranidbenim navikama u prošlosti komplicirale su taksonomsku pripadnost te se posljedično smatralo da rodu pripada najmanje 20 vrsta. Danas je općenito prihvaćena podjela roda u tri vrste: indopacifički dobri dupin (*Tursiops aduncus,* (Ehrenberg 1833)), australski dobri dupin (*Tursiops australis,* (Charlton-Robb i sur. 2011)), te obični dobri dupin (u daljnjem tekstu „dobri dupin“).

Dobri dupin (Slika *1*) odlikuje se robusnim tijelom, tamno-sivom do crnom pigmentacijom dorzalno, postupnim prijelazom na bokovima do gotovo bijele boje ventralno, umjereno zakrivljenom leđnom perajom te jasnim prijelazom između melona i rostruma (Wells i Scott 2002). Odrasle jedinke su dužine od otprilike 2 do 3,8 metara i općenito vrijedi da je veličina tijela obrnuto proporcionalna temperaturi mora. Zabilježena je varijabilnost u morfologiji s obzirom na stanište koje naseljavaju (Wells i Scott 2002), tako da se razlikuju pučinski i priobalni ekotip (Hoelzel i sur. 1998; Natoli i sur. 2004). Pučinski ekotip u pravilu je veće mase, relativno manjih peraja te tamniji. Priobalni ekotip je manje mase, relativno većih peraja i svjetliji. No, postoje i iznimke tako da su pučinski dobri dupini u istočnom dijelu Tihog oceana manje tjelesne građe od priobalnog ekotipa (Wells i Scott 2002).

Područje rasprostranjenosti dobrog dupina obuhvaća sva mora i oceane, osim polarnih područja (Leatherwood i Reeves 1990). Smatra se da je rasprostranjenost dobrog dupina uvjetovana temperaturom mora (Rice 1998). Sjeverne granice rasprostranjenosti su Ohotsko more i Kurilsko otočje u sjevernom dijelu Tihog oceana i Lofotsko otočje u sjevernom dijelu Atlantskog oceana, dok su na jugu zabilježeni u morima oko Ognjene zemlje, Južne Afrike, Australije i Novog Zelanda (Wells i Scott 2002). Na rubnim područjima rasprostranjenosti pojavljuju se sezonski, kad je temperatura mora viša. S druge strane, u priobalnim područjima umjerenog i tropskog pojasa obitavaju trajno. Zahvaljujući sposobnosti prilagodbe nastanjuju razne vrste staništa, uključujući otvorena mora, područja kontinentalnog šelfa, estuarije, kanale i ušća rijeka u koje ponekad zalaze i do 100 km uzvodno (Wilcox i sur. 1998; Wells i Scott 2002).

Slika 1. Odrasla jedinka dobrog dupina priobalnog ekotipa, fotografirana između otoka Rave i Dugog otoka (autor: Grgur Pleslić)

Dobri dupini su oportunistični u prehrani. Priobalni tip lovi uglavnom pridnenu ribu i mekušce, dok kod pučinskog tipa u prehrani dominira pelagijska riba (Leatherwood i Reeves 1990). Pučinski ekotip u pravilu živi u većim grupama koje omogućavaju suradnju i „senzornu integraciju“ prilikom traženja i lova plijena (Gowans i sur. 2008), dok priobalni ekotip obično traži i lovi plijen u manjim grupama što smanjuje kompeticiju među pripadnicima grupe (Bearzi i sur. 1997). Dobri dupini mogu razviti različite tehnike lova prilagođene vrsti staništa, odnosno trenutno dostupnom plijenu. Na primjer, u zaljevu Shark (Australija) opisano je više tehnika lova kod dobrih dupina. Pri lovu uz pješčane plaže, tjeraju ribu da se nasuče te je hvataju i sami se nasukavajući na pijesak (Sargeant i sur. 2005), tijekom lova na pridnenu ribu koriste morske spužve kojima štite rostrum od ozljeda (Mann i sur. 2008), dok u dijelovima s plitkim livadama morskih cvjetnica udaraju repnom perajom po površini, stvarajući udar dovoljne jačine da omami plijen koji se skriva među biljkama (Connor 2001). U Brazilu je opisan i slučaj suradnje između dobrih dupina i ribara prilikom lova cipala (*Mugil* spp.) s obale, gdje dupini koncentriraju i tjeraju ribu prema ribarima, dok ribari na temelju ponašanja dupina odabiru najbolji trenutak za bacanje mreže (Daura-Jorge i sur. 2012). U područjima gdje se koćari primjenjuju strategiju lova iza koćarica, iskorištavajući plijen koji je ošamućen ili ozlijeđen uslijed prolaska kroz mrežu, istjeran iz zaklona ili grabeći plijen iz mreže (Fertl i Leatherwood

1997). Ovakav način lova zabilježen je na brojnim mjestima u svijetu: Australiji (Ansmann i sur. 2012), zaljevu Savannah (SAD) (Kovacs i Cox 2014), Sredozemnom moru (La Manna i sur. 2013), kao i u Jadranu (Bearzi i sur. 1997; Fortuna 2006; Holcer 2012; Genov i sur. 2019). Redovito se bilježe slučajevi depredacije (uzimanja plijena ulovljenog u ribarske alate) na mrežama stajaćicama (Lauriano i sur. 2004; Brotons i sur. 2008; Gazo i sur. 2008) i parangalima (Hamer i sur. 2012). U blizini ribogojilišta dobri dupini love pobjeglu i divlju ribu koja se tu okuplja radi obilja nepojedene hrane koja prolazi kroz kaveze za uzgoj (López i sur. 2005).

Ženke dobrog dupina dostižu spolnu zrelost s 5 do 13 godina, mužjaci nešto kasnije, s 9 do 14 godina života (Wells i Scott 2002). Reproduktivni period kod mužjaka traje do otprilike 40. godine života, dok je kod ženki uspješna reprodukcija moguća i s 48 godina života (Wells i Scott 2002). Monogamija nije zabilježena i ženke se tijekom života pare s više mužjaka. Ženke kote jednog mladunca, uglavnom tijekom toplijih mjeseci, te brinu o njemu u prosjeku od 3 do 6 godina (Rossi i sur. 2017). Majčino mlijeko je hrana mladunaca tijekom prvih 18 mjeseci života, nakon čega mladunci počinju loviti plijen, no sisanje mlijeka može potrajati još nekoliko godina. Briga o mladuncima je za ženke energetski zahtjevna te se stoga mogu brinuti samo o jednom mladuncu, a odvajanje od majke obično se podudara s okotom novog mladunca (Wells i Scott 2002).

Dobri dupin pokazuje izrazito složene obrasce ponašanja. Iako se definicije obrazaca ponašanja razlikuju među studijama, oni se mogu svrstati u 4 osnovne grupe: lov, putovanje, druženje i odmaranje (Shane i sur. 1986). Učestalost i trajanje pojedinih obrazaca ponašanja mogu varirati u prostoru i vremenu. Na ponašanje utječu vanjski čimbenici: sezonske varijacije temperature i dostupnosti plijena, vrijeme dana, vrsta staništa; te intrinzični čimbenici: reproduktivni status i starost jedinki (Wells i Scott 2002). U pojedinim se populacijama pojavljuju specifični obrasci ponašanja kao rezultat prilagodbe na okoliš (vidi prije opisane tehnike lova). Dominantnu ulogu u usvajanju ovih specifičnih obrazaca ponašanja ima vertikalni prijenos, sa majki na mladunce (Sargeant i Mann 2009) i u manjoj mjeri horizontalni prijenos, učenjem od drugih jedinki neovisno o srodstvu ili starosti (Mann i sur. 2012). Specifični obrasci ponašanja mogu se pojaviti samo kod dijela jedinki u populaciji, što se odražava i u društvenoj strukturi populacije (Ansmann i sur. 2012; Genov i sur. 2019).

1.2. O strukturi populacije

Iako pojmovi populacije, pod-populacije, lokalne populacije, meta-populacije i zajednice spadaju među temeljne pojmove u ekologiji, nisu jednoznačno definirani (Hanski i Gilpin 1991), već ovise o kontekstu u kojem se koriste i odražavaju trenutne praktične zahtjeve odgovaranja na konkretno pitanje (Grimm i sur. 2003). Stoga je potrebno utvrditi značenje ovih pojmova kako se koriste u ovome radu.

Pojam meta-populacije nastao je u terestričkoj ekologiji i prema originalnoj definiciji označava „populaciju sastavljenu od pod-populacija koje nestaju i ponovo koloniziraju područje“ (Levins 1970). U kopnenim eko-sustavima heterogenost staništa i često jasne fizičke granice među staništima povoljnim za određenu vrstu za posljedicu imaju jasnu odvojenost među pod-populacijama koje čine meta-populaciju. Međutim, u otvorenim morskim eko-sustavima razgraničenja među pod-populacijama mobilnih vrsta uvjetovana su drugim čimbenicima te ih je često teško razlučiti. Također, zbog slabije pristupačnosti morskih eko-sustava za istraživanje i posljedično nedovoljne količine podataka, često je nemoguće utvrditi procese ekstinkcije i re-kolonizacije određenog staništa. Istovremeno, na konceptualnoj razini ovaj pojam nosi prednosti jer daje okvir unutar kojeg je moguće postavljati hipoteze i praktična pitanja važna za zaštitu vrsta (Grimm i sur. 2003). Stoga je u smislu ovoga rada primjenjiva definicija autora Reich i Grimm (1996), prema kojoj meta-populaciju sačinjavaju prostorno odvojene lokalne populacije koje zadovoljavaju sljedeće uvjete:

1. Lokalne populacije jasno se razlikuju od drugih lokalnih populacija na temelju parametara populacijske dinamike
2. Barem jedna lokalna populacije u meta-populaciji je toliko mala ili ugrožena da joj prijeti ekstinkcija
3. Lokalne populacije su u međusobnom kontaktu kroz jedinke koje dispergiraju iz područja svoje lokalne populacije
4. Jedinke koje dispergiraju imaju potencijal re-kolonizirati stanište u kojem je došlo do ekstinkcije

Za razliku od klasičnog pojma „zajednice“ koji u ekologiji označava skupine različitih vrsta koje su u međudjelovanju (Roughgarden 1989), u istraživanjima kitova ovaj pojam ima drugo značenje. Izveden je iz definicije „zajednice“ u istraživanjima čimpanzi (*Pan troglodytes,* (Blumenbach, 1775)) gdje označava sve jedinke iste vrste koje su u interakciji na zajedničkom teritoriju (Goodall 1986). U literaturi su prisutne varijacije ove definicije, međutim svima je zajedničko da jedinke u zajednici, osim što dijele prostor, sudjeluju u direktnim društvenim interakcijama (Lusseau i sur. 2006; Louis i sur. 2015; Titcomb i sur. 2015). Prema Croft i sur. (2008) zajednicu čine jedinke koje su značajno jače društveno povezane sa ostalim jedinkama iste zajednice nego sa drugim jedinkama iz populacije. Ovakva definicija pojma zajednice ima prednosti u tome što:

a) dozvoljava da zajednica nije izolirana već može biti u kontaktu sa drugim zajednicama
b) unosi kvantitativnu vrijednost, odnosno omogućuje određivanje pripadnosti zajednici statističkim metodama

U ovom radu pod pojmom „zajednice“ podrazumijevati će se definicija prema Croft i sur. (2008).

Važno je naglasiti da jedinke koje dijele isto područje obitavanja ne moraju nužno pripadati istoj zajednici. Zabilježeni su slučajevi gdje dvije zajednice dijele isti prostor, ali nisu društveno povezane (Ansmann i sur. 2012; Genov i sur. 2019). Stoga je osnovni kriterij određivanja zajednica jačina interakcija među jedinkama, a ne zajedničko područje obitavanja.

Kvantitativno opisivanje društvene strukture kod životinja je komplicirano jer „životinje ne daju intervjue i ne ispunjavaju upitnike“ (Lusseau i Newman 2004) te zbog složenosti odnosa među jedinkama koji se mijenjaju u prostoru i vremenu. Jedna od metoda istraživanja društvene strukture kod dupina je analiza društvenih mreža (eng. *social network analysis*) koja omogućava kvantitativan opis društvene strukture i utvrđivanje čimbenika koji dovode do iste (Lusseau i sur. 2006). Analizom se utvrđuju „čvorovi“ koji predstavljaju pojedine jedinke, i „veze“ među čvorovima koje predstavljaju odnose među jedinkama. Veza između dvije jedinke („par“) kvantificira se „stupnjem asocijacije“ koji je proporcija vremena koje dvije jedinke provode zajedno. Za dvije jedinke koje provode značajno više vremena nego se očekuje u nasumičnim vezama smatra se da su društveno povezane (Lusseau i sur. 2006). U istraživanjima dupina, kod kojih se promatra tek dio vremena kada jedinke izranjaju, odnosno gdje je nemoguće odrediti ukupno vrijeme koje jedinke provode skupa, ovakav način utvrđivanja stupnja asocijacije nije primjenjiv. Stoga se stupanj asocijacije među jedinkama određuje kao „polu-težinski indeks“ (eng. *half-weight index* - HWI) koji je proporcija učestalosti opažanja dvije jedinke u istoj skupini u odnosu na ukupan broj opažanja te dvije jedinke (Whitehead 2008).

1.3. Društvena struktura kod dobrog dupina

Kao društvena vrsta, dobri dupin živi u skupinama koje predstavljaju osnovnu jedinicu društvene organizacije (Barker i Berrow 2016). Veličina skupina kreće se u prosjeku od 2 do 15 jedinki i u korelaciji je s tipom staništa tako da se u plićim, priobalnim područjima susreću manje skupine dok su u dubljim, otvorenim područjima češće velike skupine, ponekad sa više stotina jedinki (Shane i sur. 1986). U estuariju rijeke Sado (Portugal) prosječna veličina skupina je 7,8 jedinki (Augusto i sur. 2012), kod Balearskih otoka (Španjolska) 6,7 jedinki (Gonzalvo i sur. 2014), kod Antalyje (Turska) 7,3 jedinki (Baş i sur. 2017), dok su u Jadranu utvrđene prosječne veličine skupina od 6,3 jedinki kod otoka Visa (Holcer 2012), od 5,9 do 9,3 jedinki u Kvarneriću (Pleslić i sur. 2015), 6,5 jedinki u teritorijalnom moru Crne Gore (Miočić-Stošić i sur. 2020) i 8,0 jedinki u Tršćanskom zaljevu (Genov i sur. 2008). Među glavne čimbenike koji utječu na veličinu skupina ubrajaju se dostupnost plijena, obrana od predatora, ponašanje i starosni sastav (Barker i Berrow 2016). U plićim, priobalnim područjima fiziografska i stanišna raznolikost doprinosi predvidivoj rasprostranjenosti plijena te stoga lov u manjim skupinama smanjuje kompeticiju među pripadnicima skupina (Bearzi i sur. 1997). U otvorenim područjima s jednoličnim fiziografskim obilježjima plijen je koncentriran u veća jata koja je teže pronaći. U ovakvim uvjetima suradnja i senzorna integracija, koje su moguće kod većih skupina, doprinose uspješnosti pronalaska i lova plijena (Shane i sur. 1986). Osim zaštite od predatora, kooperacija kod većih skupina pospješuje i brigu o mladuncima (Shane i sur. 1986). Značajno veće skupine s mladuncima u odnosu na skupine samo odraslih jedinki utvrđene su kod Drowned Cayes otočja (Belize) (Kerr i sur. 2005), estuariju rijeke Shannon (Irska) (Barker i Berrow 2016), estuariju rijeke Sado (Portugal) (Augusto i sur. 2012), Tunisu (Benmessaoud i sur. 2013) te u Jadranu u Kvarneriću (Bearzi i sur. 1997) i kod otoka Visa (Holcer 2012). Nasuprot prednostima, veće skupine doprinose pojačanoj kompeticiji za resurse (Lodi 2012) i reproduktivne ženke (Connor i Krützen 2015) te prijenosu patogena među pripadnicima skupine (Ebensperger i sur. 2012).

Skupine dobrih dupina mijenjaju sastav više puta tijekom dana te se stoga u literaturi ovakav način osnovne društvene organizacije naziva fisijsko-fuzijskim društvom (Connor i sur. 2000). Primjerice, u Kvarneriću je izmjereno prosječno trajanje između dvije izmjene sastava skupine od 54,4 min (SE = 2,17) s rasponom od 3 do 543 minute (Bearzi i sur. 1997). Ipak, pojedine jedinke ponekad formiraju dugotrajne, višegodišnje asocijacije. Tako mužjaci formiraju parove ili tria koji mogu ostati stabilni i više desetljeća (Connor i sur. 2001; Connor i Krützen 2015). Višegodišnje asocijacije među jedinkama zabilježene su i u akvatoriju Visa

(Holcer 2012). Također, mlađe odrasle jedinke do dostizanja spolne zrelosti duže vrijeme ostaju u istim skupinama (Baker i sur. 2018).

Unatoč dinamičnim izmjenama sastava skupina na dnevnoj bazi, dobri dupini često formiraju zajednice. Te zajednice sačinjavaju jedinke koje, gledano na duže razdoblje, imaju značajno višu stopu interakcija s drugim pripadnicima iste zajednice nego s drugim jedinkama. Niska stopa interakcija među jedinkama različitih zajednice može jednostavno odražavati odvojena područja obitavanja. Tako je u zaljevu Tampa (Florida, SAD), na području manjem od 900 km^2, opisano pet zajednica dobrih dupina od kojih samo dvije koriste isti prostor (Urian i sur. 2009), dok su u Normandijsko-Bretonskom zaljevu opisane tri zajednice sa zasebnim područjima obitavanja (Louis i sur. 2015). No, zabilježeni su i slučajevi gdje dvije zajednice dijele isti prostor, ali nisu društveno povezane (Ansmann i sur. 2012; Genov i sur. 2019). Odlike jedinki koje utječu na njihovu pripadnost pojedinim zajednicama uključuju spol (Connor i sur. 2000), starost (Lusseau i Newman 2004), srodstvo (Wiszniewski i sur. 2010), ponašanje (Krützen i sur. 2005), tehnika lova (Daura-Jorge i sur. 2012) te privrženost staništu (Lusseau i sur. 2006).

1.4. Područje obitavanja

Područje obitavanja je ono područje koje jedinka, skupina ili zajednica koriste u redovnim aktivnostima: lovu, parenju i brizi o mladuncima (Burt 1943). Prema novijim definicijama područje obitavanja predstavlja model koji opisuje kako jedinke doživljavaju i koriste prostor te stvaraju kognitivnu mapu područja koju dugotrajno pamte, s informacijama o važnim koridorima i lokacijama resursa (Oshima i Santos 2016). Općenito vrijedi da područje obitavanja jedinke ovisi o trenutnim fiziološkim zahtjevima, te o prisutnosti i prostornoj distribuciji drugih jedinki iste vrste, predatora i resursa (Passadore i sur. 2018). Tako u područjima niske produktivnosti i nejednoliko raspoređenih resursa jedinke u pravilu prelaze veće udaljenosti što rezultira manjom privrženošću određenom području i posljedično većim područjem obitavanja (Silva i sur. 2008). Nasuprot tome, visoka privrženost manjem području obitavanja javlja se u uvjetima kada je produktivnost visoka, a resursi predvidivi. Ovakva pravilnost utvrđena je kod različitih svojti, uključujući kukce (Switzer 1997), ptice (Habel i sur. 2016), morske pse (Knip i sur. 2012) i kopnene sisavce (Edwards i sur. 2009).

Poznavanje područja obitavanja jedinke ili zajednice jedna je od ključnih informacija u ekologiji i konzervacijskoj biologiji (Fleming i Calabrese 2017). Postoje različite metode određivanja područja obitavanja, a dijele se na geometrijske i statističke (Powell 2000; Fleming i sur. 2015). Odabir prikladne metode ovisi o istraživanoj vrsti, raspoloživim podatcima i ciljevima istraživanja.

Najjednostavnija je geometrijska metoda određivanja najveće linearne udaljenosti (eng. *maximum linear distance* – MLD) između lokacija na kojima je jedinka opažena. Nedostatak ove metode je što ne daje informaciju o površini područja obitavanja ili načinu korištenja staništa unutar tog područja. Ipak, može biti primjenjiva u linearnim staništima, primjerice u uskim kanalima ili rijekama (Balmer i sur. 2008).

Geometrijska metoda najmanjeg konveksnog poligona (eng. *minimum convex polygon* – MCP) područje obitavanja određuje kao poligon omeđen najisturenijim lokacijama opažanja jedinke. Ovom metodom moguće je utvrditi površinu područja obitavanja, no ona ne uzima u obzir heterogenost u načinu korištenja staništa unutar tog područja (Katajisto i Moilanen 2006). Nadalje, MCP metoda kod malog broja opažanja podcjenjuje područje obitavanja (eng. *negative bias*) i podložna je greškama kada postoje pretjerano isturene lokacije opažanja, na primjer kada jedinka privremeno napusti područje obitavanja (Urian i sur. 2009). Stoga u slučajevima kada jedinke povremeno izlaze izvan redovnog područja obitavanja ili kod migratornih vrsta ova metoda preuveličava područje obitavanja (eng. *positive bias*). S druge strane, ovo je jedna od najstarijih, najjednostavnijih i najraširenijih metoda te stoga omogućava usporedbe među studijama (Powell 2000; Nilsen i sur. 2008).

Kao novija metoda u analizi područja obitavanja koristi se procjenitelj gustoće jezgre (eng. *kernel density estimator* – KDE). Ovo je statistička, neparametrijska metoda koja procjenjuje funkciju gustoće vjerojatnosti nalaženja jedinke u prostoru, te stoga ima brojne prednosti u odnosu na ranije metode. Primjenjiva je u širokom rasponu slučajeva jer uzima u obzir heterogenost u distribuciji lokacija opažanja, što je u stvarnosti najčešći slučaj, i ne zahtjeva prethodno poznavanje bioloških procesa koji dovode do heterogenosti (Fleming i Calabrese 2017). U primjeni ove metode lokacije opažanja moraju biti neovisne. Kada su lokacije opažanja auto-korelirane, kao u slučajevima kontinuiranog praćenja, KDE metoda podcjenjuje područje obitavanja (eng. *negative bias*). Nadalje, KDE metoda omogućava modeliranje utjecaja pojedinih lokacija opažanja na konačan oblik procijenjenog područja obitavanja, primjenom tzv. „parametra zaglađivanja“ (eng. *smoothing parameter*) (Worton 1989) čime se može regulirati finoća prikaza područja obitavanja. Kao statistička metoda, KDE daje i informaciju o vjerojatnosti nalaženja jedinke unutar područja obitavanja te tako ukazuje na pojedina područja od veće ili manje važnosti za jedinku. S obzirom na vjerojatnost pronalaženja jedinke, u istraživanjima dupina općenito je prihvaćena podjela područja obitavanja na: jezgru područja obitavanja (eng. *core area*) gdje jedinka provodi 50 % vremena (50 % KDE), i na ukupno područje obitavanja (eng. *home range*) gdje jedinka provodi 95 % vremena (95 % KDE) (Powell 2000; Urian i sur. 2009; Titcomb i sur. 2015; Louis i sur. 2017).

Određivanje područja obitavanja u istraživanjima dupina problematično je iz dva razloga. Kao prvo, zbog činjenice da je gotovo nemoguće dovoljno dugo i kontinuirano pratiti jedinke u njihovom kretanju prostorom. Kao drugo, područja istraživanja često su ograničena logističkim čimbenicima i ne obuhvaćaju cijelo područje obitavanja istraživane jedinke ili zajednice. Stoga su područja obitavanja u brojnim istraživanjima rezultat prostorne i vremenske distribucije istraživačkog napora i ne odražavaju stvarno područje obitavanja (Urian i sur. 2009). Zbog navedenih poteškoća potrebna su dugotrajna, kontinuirana istraživanja te dijeljenje podataka prikupljenih u različitim područjima istraživanja (Cheney i sur. 2013).

Na područje obitavanja utječu privrženost području (eng. *site-fidelity*) i rezidentnost (eng. *residency*). Rezidentnost se definira kao trajanje boravka jedinke u određenom području (Wells i Scott 1990), dok privrženost području označava učestalost korištenja određenog područja (Baird i sur. 2008). Ova dva pojma mogu se smatrati sinonimima u slučajevima kada je jedinka ili zajednica dugotrajno rezidentna u određenom području. Razlika nastaje u slučajevima kada se različita područja koriste u različito vrijeme, primjerice kod migratornih vrsta. Tako grbavi kitovi (*Megaptera novaeangliae,* (Borowski 1781)) pokazuju jaku privrženost odvojenim područjima hranjenja i razmnožavanja, ali samo sezonsku rezidentnost u tim područjima. Privrženost području i rezidentnost imaju praktičnu primjenu u konzervacijskoj biologiji jer ukazuju na područja od naročite važnosti i kada ukupno područje obitavanja nije točno utvrđeno (Dinis i sur. 2016).

1.5. Područja obitavanja dobrog dupina

Jedinke i zajednice dobrog dupina pokazuju različite stupnjeve rezidentnosti i privrženosti određenom području tako da im se i područja obitavanja razlikuju. Niža privrženost određenom području te posljedično veća područja obitavanja kod dobrih dupina koji naseljavaju otvorena mora od onih u koji naseljavaju priobalna područja dovodi se u vezu s dostupnošću plijena, odnosno nižom produktivnošću oceanskih staništa u odnosu na priobalna (Silva i sur. 2008). Prema dostupnoj literaturi, područja obitavanja priobalnih jedinki i zajednica utvrđena 95 % KDE metodom variraju od nekoliko desetina do nekoliko stotina km^2. Među najmanjim područjima obitavanjima jedinki dobrih dupina su ona u Južnoj Karolini (SAD), gdje variraju od 17,2 km^2 do 98,9 km^2 (Gubbins 2002), dok su među najvećima ona na Azorima gdje je utvrđena prosječna veličina područja obitavanja jedinki od 437,2 km^2 (Silva i sur. 2008). Od područja obitavanja zajednica najmanje (33,5 km^2) je utvrđeno u području oko otoka Sein (Francuska) (Louis i sur. 2017), a među najvećima su područja obitavanja dvije zajednice (410 km^2 i 529 km^2) u zaljevu Tampa na Floridi (SAD) (Urian i sur. 2009). U više istraživanja utvrđene su i razlike u veličini područja obitavanja jedinki ovisno o spolu i reproduktivnom statusu. Načelno, mužjaci imaju veća područja obitavanja (Nekolny i sur. 2017; Wells i sur. 2017), no zabilježene su i iznimke. Tako u Južnoj Karolini (SAD) ženke imaju veća područja obitavanja od mužjaka, a razlika je izraženija kod ženki s mladuncima (Gubbins 2002).

Unatoč tome što kod priobalnih zajednica dobrog dupina postoji privrženost određenom području, neke jedinke prevaljuju velike udaljenosti. Primjerice, u Crnom moru su zabilježena opažanja istih jedinki na lokacijama udaljenim 325 km (Gladilina i sur. 2016), u Grčkoj 265 km (Bearzi i sur. 2011) i u Ligurskom moru 427 km (Gnone i sur. 2011). No, udio jedinki iz priobalnih rezidentnih zajednica koje poduzimaju ovakva putovanja je nizak. Istraživanjem u Ligurskom moru metodom najveće linearne udaljenosti utvrđeno je da 80 % jedinki prelazi udaljenosti do 80 km, dok su udaljenosti od preko 200 km utvrđene za 2 % jedinki (Gnone i sur. 2011). Slično tome, u Grčkoj su istom metodom utvrđene udaljenosti od preko 120 km za 3 % jedinki obuhvaćenih istraživanjem (Bearzi i sur. 2011), dok su udaljenosti od preko 300 km zabilježene za manje od 1 % foto-identificiranih jedinki u Crnom moru (Gladilina i sur. 2016). Također je utvrđeno da velike udaljenosti prevaljuju uglavnom mužjaci (Bearzi i sur. 2011), što je u skladu s općim trendom kod sisavaca (Greenwood 1980).

1.6. Dobri dupin u Jadranskom moru

Dobri dupin jedina je vrsta morskih sisavaca koja trajno naseljava cijelo Jadransko more (Holcer i sur. 2014). Procijenjena brojnost za cijeli Jadran, utvrđena istraživanjima iz zraka metodom linijskih transekata provedenima tijekom 2010. i 2013. godine, iznosi 5700 jedinki uz 95 % interval pouzdanosti od 4300 do 7600 (Fortuna i sur. 2018). Navedena procjena brojnosti nije korigirana za faktore dostupnosti i vidljivosti te je stoga stvarna brojnost veća.

Istim istraživanjem utvrđena je relativna gustoća od 0,042 jedinke po km^2 za cijeli Jadran. No, gledajući zasebno 2010. i 2013. godinu, najviše relativne gustoće utvrđene su u obje godine u sjevernom Jadranu, dok su u drugim dijelovima niže i varijabilne. Prema Fortuna i sur. (2018), viša relativna gustoća u sjevernom Jadranu može biti odraz veće produktivnosti staništa dok varijabilnost u južnom Jadranu moguće odražava priljev tranzijentnih jedinki.

Do sada su u istočnom Jadranu provedena istraživanja dobrih dupina u područjima cresko-lošinjskog arhipelaga (Bearzi i sur. 1997; Fortuna 2006; Pleslić i sur. 2015), Murterskog mora (Impetuoso i sur. 2003; Kammigan i sur. 2008), viškog i lastovskog akvatorija (Holcer 2012), Tršćanskog zaljeva (Genov i sur. 2008) i u teritorijalnom moru Crne Gore (Miočić-Stošić i sur. 2020), a rezultati temeljeni na foto-identifikacijskim i genetskim podatcima idu u prilog hipotezi o meta-populaciji (Holcer i sur. 2014). Posljednje procjene brojnosti rezidentnih zajednica ukazuju na to da u cresko-lošinjskom arhipelagu obitava od 112 jedinki (95 % CI = 94-150) u 2008. godini do 310 jedinki (95 % CI = 265-392) u 2006. godini (Pleslić i sur. 2015), u tršćanskom zaljevu od 38 jedinki (95 % CI = 34-47) u 2004 godini do 108 jedinki (95 % CI = 84-163) u 2006. godini (Genov i sur. 2008), u području otoka Visa od 371 jedinke (95 % CI = 325-442) u 2009. godini do 474 jedinke (95 % CI = 352-683) u 2010. godini (Holcer 2012), a u teritorijalnom moru Crne Gore 90 jedinki (95 % CI = 71-152) u 2013. godini (Miočić-Stošić i sur. 2020). Usporedbom kataloga leđnih peraja cresko-lošinjskog arhipelaga (preko 600 jedinki) s onim iz tršćanskog zaljeva (otprilike 120 km sjeverno) nije nađena ni jedna jedinka opažena u oba područja (Genov i sur. 2008), usporedba s katalogom iz područja Murterskog mora (otprilike 70 km južno) otkriva samo sedam jedinki viđenih u oba područja tijekom pet godina (Fortuna 2006; Pleslić i sur. 2015), dok usporedba s katalogom iz viškog i lastovskog arhipelaga (otprilike 200 km južno) ne otkriva ni jednu jedinku opaženu u oba područja (Holcer 2012). Ovi rezultati ukazuju na izoliranost lokalnih zajednica, no njihova područja obitavanja i razine društvene povezanosti dosadašnjim istraživanjima nisu utvrđene.

Istraživanje genetičke strukture populacije nadopunjuje rezultate istraživanja temeljenih na foto-identifikaciji i pokazuje da je jadranska populacija dobrog dupina odvojena od onih iz susjednih područja (Tirensko, Jonsko i Egejsko more) (Gaspari i sur. 2013). Isto istraživanje otkriva da, iako su dobri dupini prisutni u cijelom Jadranskom moru, postoji genetička diferencijacija između jedinki sa zapadne i istočne strane, kao i između sjevernog te srednjeg i južnog Jadrana, što dodatno potkrepljuje pretpostavku o metapopulaciji. Nadalje, lokalna populacija u sjevernom Jadranu djeluje kao izvorišna populacija za unos gena u druga područja dok ženke imaju glavnu ulogu kao medijatori protoka gena.

2. CILJEVI I PREGLED DISERTACIJE

Ciljevi ove disertacije su:

1. *Istražiti prostornu i društvenu strukturu populacije dobrog dupina duž istočne obale Jadranskog mora kako bi se potvrdila pretpostavka o zasebnim zajednicama te odredila njihova područja obitavanja i razina društvene povezanosti.*

   Ovaj cilj obrađen je u znanstvenom radu **1**, koji prikazuje rezultate analiza društvene mreže i područja obitavanja te modeliranja vjerojatnosti migracija jedinki, temeljenih na foto-identifikacijskim podatcima prikupljenim tijekom pet ljetnih sezona.
2. *Istražiti čimbenike koji utječu na društvenu strukturu i područja obitavanja dobrog dupina u istočnom Jadranu.*

   Ovaj cilj obrađen je u znanstvenom radu **2**, koji opisuje utjecaj intrinzičnih (spol i dob) i ekstrinzičnih čimbenika (nautički promet i koćarenje) na društvenu strukturu i varijacije u područjima obitavanja dobrog dupina.
3. *Opisati demografske parametre zajednice dobrih dupina u do sada neistraženom području sjeverne Dalmacije.*

   Ovaj cilj obrađen je u znanstvenom radu **3**, koji daje rezultate analiza prisutnosti, veličine skupina i privrženosti području te procjene brojnosti, migracija i godišnjih stopa preživljavanja za zajednicu dobrih dupina u području sjeverne Dalmacije.

3. ZNANSTVENI RADOVI

3.1. Znanstveni rad 1

Pleslić G, Rako-Gospić N, Miočić-Stošić J, Blazinić Vučur T, Radulović M, Mackelworth P, Frleta-Valić M, Holcer D (2019). Social structure and spatial distribution of bottlenose dolphins (*Tursiops truncatus*) along the Croatian Adriatic coast. Aquatic Conservation: Marine and Freshwater Ecosystems 29(12): 2116-2132.

3.2. Znanstveni rad 2

Rako-Gospić N, Radulović M, Vučur T, Pleslić G, Holcer D, Mackelworth P (2017). Factor associated variations in the home range of a resident Adriatic common bottlenose dolphin population. Marine Pollution Bulletin 124(1): 234-244.

3.3. Znanstveni rad 3

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RESEARCH ARTICLE

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Social structure and spatial distribution of bottlenose dolphins (*Tursiops truncatus*) along the Croatian Adriatic coast

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Abstract

1. Previous studies suggest that the common bottlenose dolphin population in the Croatian Adriatic Sea is structured into distinct local communities. However, their home ranges and levels of interaction remain unknown.
2. Dedicated boat-based surveys were conducted seasonally, in three adjacent study sites from 2013 to 2017. Photo-identification data were used to identify distinct local communities by relating the social structure descriptors to the home ranges of individual animals, and to determine the community home ranges and identify the levels of interactions between them.
3. The overlaps between the home ranges of individuals (50 and 95% kernel density estimators [KDE]) were positively correlated to association strengths between them. Three distinct communities were identified by the hierarchical cluster analysis. The individuals' 95% KDE home range overlaps and association strengths were significantly higher within the three communities than between them, indicating both social and spatial segregation.
4. The 95% KDE home ranges of the communities showed very low to no overlap. The individuals ranged mainly centrally within the home range of their respective community. The probabilities of movement, expressed as lagged identification rates, were significantly higher within than between community home ranges. However, 37 out of 1024 identified individuals were observed in more than one community home range, indicating that the communities are not isolated.
5. Four out of the six Sites of Community Importance currently in place within the Croatian Adriatic Sea lie within the home ranges of the three local bottlenose dolphin communities. Once these sites are declared as Special Areas of Conservation, the management scheme will need to accommodate for differences in the spatial and social ecology of these communities, and environmental and anthropogenic factors acting upon them. The results of this work provide baseline information for such tailored management.

KEYWORDS

Adriatic Sea, association index, bottlenose dolphin, community, conservation, home range, social structure, *Tursiops truncatus*

1 | INTRODUCTION

In segregated cetacean populations, distinct communities can be exposed to different threats or can be differently affected by the same threat depending on their level of isolation. Closed communities are less resilient to environmental stressors than the open ones (Papale et al., 2016). In open communities, frequent interactions with transient individuals can result in higher genetic diversity and knowledge transfer (Rendell & Whitehead, 2001), which lead to increased population fitness (Papale et al., 2016). Therefore, information on population social structure, home ranges of distinct communities, and interactions between them is crucial for effective conservation of cetaceans (Ingram & Rogan, 2002; Parra, Corkeron, & Marsh, 2006), as it can be used as covariates to provide more robust population dynamics models (Lusseau et al., 2006) and test for differences between communities. For instance, the defined community home ranges can be used as sampling units while detected movements between them can help discern mortality from emigration to adjacent areas, ultimately leading to more exact mark-recapture abundance estimates for each community. However, in studies of highly mobile cetaceans, logistical constraints often prevent surveys of their entire home range. As a result, estimated home ranges are biased downwards and do not accurately represent the actual situation (Nekolny et al., 2017; Silva et al., 2008), which can negatively reflect on the efficiency of conservation measures (Wilson, Reid, Grellier, Thompson, & Hammond, 2004). To tackle this problem, large-scale studies and data sharing among research groups is suggested (Cheney et al., 2012).

The common bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821; hereafter bottlenose dolphin) is known to live in fission–fusion societies in which associations between individuals can change within hours or days (Connor, Wells, Mann, & Read, 2000). Nevertheless, communities (i.e. groups of individuals that share association and ranging patterns across longer time spans) have been described in many studies of coastal bottlenose dolphin populations (Urian, Hofmann, Wells, & Read, 2009; Lusseau et al., 2006; Wells, Scott, & Irvine, 1987). Structuring of populations into communities is the result of biotic and abiotic factors. The former include prey availability (Pace, Pulcini, & Triossi, 2012), predation risk (Heithaus & Dill, 2002), presence or absence of preferred associations (Lusseau et al., 2006), natal philopatry (Rako-Gospić et al., 2017), behavioural homophily (Cantor & Whitehead, 2013), and human activities such as fisheries (Ansmann, Parra, Chilvers, & Lanyon, 2012; Bearzi, Politi, & Sciara, 1999; López & Shirai, 2008) and boat traffic (Bejder et al., 2006; Fertl & Leatherwood, 1997; Pirotta, Merchant, Thompson, Barton, & Lusseau, 2015; Rako-Gospić et al., 2017). The latter abiotic factors include oceanographic characteristics (Wiszniewski, Allen, & Möller, 2009) and landscape complexity (Lusseau et al., 2003). Bottlenose dolphin communities vary in home range sizes, from tens of km^2 (Louis et al., 2017) to hundreds of km^2 (Rako-Gospić et al., 2017). They also have different levels of spatial separation, from those adjacent, but spatially separated (Urian et al., 2009), to those that maintain social segregation despite considerable home range overlap (Chilvers & Corkeron, 2001; Genov, Centrih, Kotnjek, & Hace, 2019; Lusseau et al., 2006).

The bottlenose dolphin is the only cetacean species regularly inhabiting the northern and central Adriatic Sea (Holcer, Fortuna, & Mackelworth, 2014). Studies conducted in Kvarner (K) region and Vis-Lastovo (V) region (Figure 1) indicate the existence of distinct communities that show various degrees of site fidelity. The community in the K region has been extensively studied since 1987. Bearzi, Notarbartolo-di-Sciara, and Politi (1997) photo-identified 107 individuals up to 1994 and noted their multi-year site fidelity to an 800 km^2 study area. The subsequent, spatially expanded (2,000 km^2) study of Fortuna (2006) on the same community reported a decline in abundance, from 168 individuals (95% confidence interval [CI] 132–229) in 1995 to 102 individuals (95% CI 86–127) in 2003. The latest study of this community encompassed 1600 km^2 and showed a recovery, with abundance estimates varying between 112 (95% CI 94–150) and 310 (95% CI 265–392) individuals between 2004 and 2011 (Pleslić et al., 2015). All three studies conclude that the home range of the K community extends beyond the respective surveyed areas. Furthermore, the comparison of Blue World Institute's bottlenose dolphin dorsal fin catalogue from the K region with the catalogues of animals photographed in V region (200 km to the south), Montenegrin Sea (400 km to the south), Ravenna region (130 km to the west), and Gulf of Trieste (140 km to the north, Genov, Wiemann, & Fortuna, 2009), revealed no matches. Comparison with the catalogue from Murter Sea (80 km to the south; Figure 1) revealed five matches out of 594 catalogued individuals (0.8%; Pleslić et al., 2015), indicating limited exchange between different Adriatic regions.

The study conducted in the V region since 2007, around 200 km south from the K (Figure 1), suggests the existence of another distinct local community (community V) with abundance estimated at around 400 individuals, but comprising a relatively low proportion of resident individuals (*N* = 109; Holcer, 2012). The comparison of dorsal fin catalogue from the V region with the catalogues from other areas in the Adriatic Sea (Gulf of Trieste, Kvarner, Murter Sea, Montenegrin Sea, and Ravenna regions) found no matches. Furthermore, individuals in the southernmost part of the V region exhibited different ranging and association patterns, indicating that another local community may exist further south (Holcer, 2012).

Genetic studies corroborate the presence of the population structuring conclusions drawn from the photo-identification data. Gaspari et al. (2015) found a fine-scale genetic differentiation between north and central-south, and between east and west Adriatic. The same study identified a significant rate of gene flow from the north Adriatic to central-south Adriatic with females acting as main gene flow mediators.

The European Union Habitat Directive (Council Directive 92/43/EEC) lists bottlenose dolphins in Annex II and all cetaceans in Annex IV. These listings require the establishment of Special Areas of Conservation (SACs) with appropriate conservation measures in place that address the ecological requirements of this species. Within the Croatian Adriatic Sea, six Sites of Community Importance (SCIs) for bottlenose dolphins exist as part of the Natura 2000 ecological

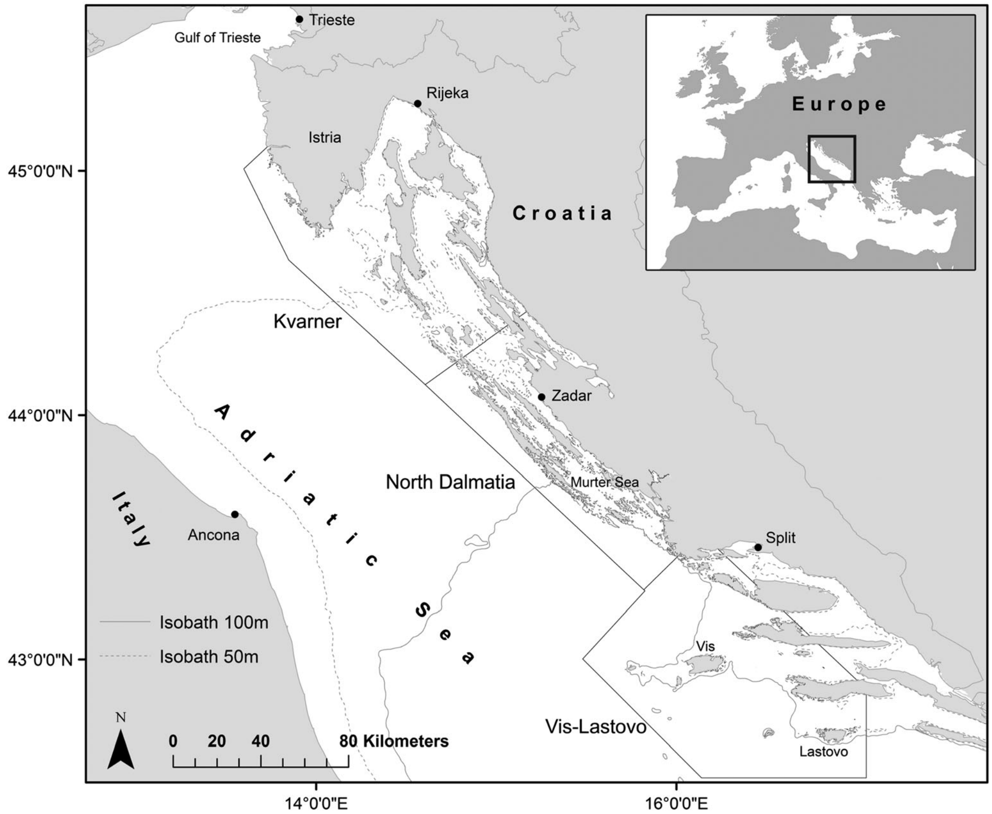

FIGURE 1 Study area with indicated subdivision into the three study sites: the northern study area ('Kvarner'), the central area ('North Dalmatia'), and the southern area ('Vis-Lastovo')

network (Figure 10; European Environment Agency), with the prospect to be declared as SACs by 2020. The published studies suggest that the bottlenose dolphin population in the Croatian Adriatic Sea is structured into distinct resident communities. However, their actual home ranges and levels of interactions as well as how the current SCIs correspond to the home ranges of these communities, remain unknown.

In 2013, a new study was started in the region of North Dalmatia (ND), closing the gap in survey effort between the two existing study sites (Figure 1). In this paper, photo-identification data from the three contiguous study sites (K, ND, and V) are used to: a) describe social structuring into distinct communities, b) determine home ranges of the communities, c) quantify levels of interactions between communities, and d) contribute to bottlenose dolphin conservation in the Adriatic by informing the future management on how the SCIs spatially correspond to home ranges of communities.

2 | METHODS

2.1 | Study area

The study area is located along the eastern Adriatic coast within the Croatian territorial sea. It stretches from the Istrian peninsula in the north, to the island of Lastovo in the south, encompassing approximately 19,000 km^2 (Figure 1). It is characterized by a typical Mediterranean climate, with average sea temperature of 25°C in the summer (Penzar, Penzar, & Orlić, 2001), predominantly rocky shores, steep slopes, and a variety of seabed types (Alfirević, 1981). The K and ND regions encompass highly diverse archipelagos with numerous islands and channels, and water depths averaging <100 m (Figure 1). The V region corresponds mostly to the open sea with water depths exceeding 100 m (Figure 1).

2.2 | Field procedures

Daily visual surveys were conducted in search of bottlenose dolphins during the May–October periods from 2013 to 2017, by three research teams operating in the K, ND, and V regions (Figure 1). All three teams used similar research vessels: rigid hull inflatables from 5.2 to 5.8 metres in length and powered by 60–100 HP outboard engines. All groups applied the same field and data handling protocols. Overall survey effort aimed to achieve continuous coverage across the whole study area. Daily survey tracks were chosen *ad libitum*, depending on the prevailing weather conditions, while trying to survey all parts of the study area at least once each month. Surveys were considered to be on effort when the following conditions were met: a) at least two researchers were actively looking for dolphins in a standing position, b) sea-state was <3 Beaufort scale, c) boat speed between 12 and 15 knots, and d) visibility was not obscured by fog or rain. Upon spotting dolphins, the vessel approached the group.

Location and time were noted and the sighting procedure was initiated following the guidelines of Würsig and Jefferson (1990). All individuals observed to be in apparent association either by proximity (usually <100 m), engagement in same activity or maintaining the same swimming direction were considered to form a group. If the group composition changed, with individuals joining or leaving, a new group was noted. Effort was made to take photographs of both sides of the dorsal fin for all the individuals present in each group, when possible. The sighting procedure was terminated when all individuals were believed to have been photographed or when the weather conditions severely deteriorated. The navigation data were recorded using various GPS devices with ±7 m accuracy. The photographs were taken using Canon EOS 40D, EOS 7D, and EOS 5D digital SLR cameras equipped with Canon EF 70–200 mm F/2.8 L USM lenses.

2.3 | Photo-identification

Only photographs that were in focus, well lit, showing the whole dorsal fin, and where the angle of the dorsal fin to the camera was approximately perpendicular were considered of sufficient quality to be used for photo-identification. Only individuals with distinctive primary markings, e.g. notches, cuts, mutilations on the dorsal fin edges, were considered reliably identifiable and used for all subsequent analyses. Identified individuals were assigned to age classes: adults, juveniles, calves, and newborns (see Pleslić et al., 2015 for details on age-class definitions). Individuals for which a photograph of genital area was available were classed as females or males. Those repeatedly observed in association with a newborn or a calf were classed as females. Individuals known as adults for more than 12 years, but never seen with a calf were classed as probable males (Rako-Gospić et al., 2017). All others were classed as unknown sex. The information on the group, date, time, and location were added to each photograph. The image databases from all three research teams (study sites) were cross-examined by at least one experienced researcher from each team for potential matches and then merged into a unified catalogue from which a capture history dataset was created. Photoshop Lightroom 6.0 (Adobe, 2017) with custom built add-ons was used for matching photographs, compiling catalogues and merging with the ancillary group and navigation data.

2.4 | Social structure analyses

To test whether the bottlenose dolphin population sampled across the whole study area was divided into discrete communities, an analysis of social structure was conducted using the SOCPROG 2.8 software (Whitehead, 2009). One of the aims of this study was to test the correlation between the social structure descriptors and the home range estimates of individual animals, which required a minimum of 10 observations per individual. Hence, only individuals seen on 10 or more occasions were included. This is double the minimum of five observations suggested by Whitehead (2008), thus reducing the bias in the social structure parameters due to infrequently sighted individuals. Non-adults were excluded from the social structure and home range analyses as their associations and sighting locations are confounded with those of their mothers.

Individuals present in the same group were considered to be associated. Those individuals associated across more groups within a day were considered as being associated once in that day to avoid pseudo-replication. To avoid demographic effects, sampling period was set to one day (Whitehead, 2008). The half-weight index (HWI) was used as a measure of association strength between pair members. The HWI represents the proportion of time the two individuals are associated, ranging from ‘0’ for pairs never seen together, to ‘1’ for pairs always seen together. The HWI was used for its resilience to bias caused by potential incomplete sampling (Cairns & Schwager, 1987) and its ubiquitous use in similar studies, which makes comparisons possible.

Pearson's correlation coefficient r was calculated to examine if the HWI values adequately represent social structure; value of ‘0’ meaning no representation and ‘1’ meaning perfect representation (Whitehead, 2008). Furthermore, social differentiation (S) and the mean number of associations per individual (H) were calculated to test the power to reject the null hypothesis of homogenous associations. When S is 1 or higher, the association indices are highly variable and the product $S^2*H > 5$ suggests the rejection of the null hypothesis (Whitehead, 2008).

The division into communities was explored by running the hierarchical cluster analysis on the HWI matrix using the average linkage method (Whitehead, 2008). The HWI value at which the modularity (Q) is maximized was used as a cut-off (Newman, 2004) to visually represent communities on a dendrogram. A Q value > 0.3 was considered to represent meaningful division into communities (Newman, 2004). The cophenetic correlation coefficient was calculated as an indicator of how accurately the dendrogram represents the association index matrix. A cophenetic correlation coefficient of 0.8 or above is generally considered to indicate a good representation (Bridge, 1993). Individuals were then assigned to a corresponding community based on the results of the hierarchical cluster analysis. Mean HWI values were calculated for each community and between communities, and tested for significant differences with the Mann–Whitney test.

To visually represent the community structure, a network diagram was created applying Force Atlas algorithm in Gephi 0.9.2 (Bastian, Heymann, & Jacomy, 2009). The diagram aggregates individuals based on association strength between them, and represents ‘eigenvector centrality’ for each individual. The ‘eigenvector centrality’ was calculated in SOCPROG 2.8 (Whitehead, 2009) and represents how well an individual is connected to others in the network by combining its number of association with the number of associations of its associates (Newman, 2004). Only meaningful associations are represented, i.e. those with HWI higher than twice the average HWI of the whole sample (Genov et al., 2019; Wiszniewski, Brown, & Möller, 2012).

To test whether preferred or avoided associations exist within the whole sample and within each community, the Monte Carlo test was performed by permuting the data matrix and comparing results with the observed data matrix (Bejder, Fletcher, & Bräger, 1998). In this test, lower standard deviation (SD) and coefficient of variation values from the permuted data matrix than those from the observed data matrix imply existence of preferred associations, and higher proportions of non-zero associations from the permuted data matrix than those from the observed data matrix imply existence of avoidance between pairs (Whitehead, 2008). Furthermore, pairs with association strengths either significantly higher than 97.5%, or lower than 2.5% of their random associations were detected (Bejder et al., 1998). The test was run with 15,000 permutations and 1,000 trials per permutation to ensure the stability of the *P* values.

2.5 | Home ranges

To determine the minimum number of observations per individual needed to estimate the home ranges, minimum convex polygons (MCPs) of individuals were plotted against number of observations per individual (area–observation curve; Silva et al., 2008). The MCP method is sensitive to outlier locations which result in unrealistically large areas (Harris et al., 1990; Urian et al., 2009). Therefore, sighting locations furthest away from the harmonic mean of all sightings of each individual were detected by harmonic mean outlier method (White & Garrot, 1990) and removed from the sample. The areas of individual MCPs were then calculated and the bootstrap test was run on the series of samples with increasing number of observations per individual (Silva et al., 2008). The results were plotted on an area–observations curve, which showed an increase of the MCP areas for samples of up to nine observations and no increase for samples of 10 or more (Figure 2). Therefore, all subsequent home range analyses (and social structure analyses) were performed on the dataset with 177 individuals seen on 10 or more occasions.

To ensure independence of sighting locations, for individuals seen more than once in a day, only the first sighting location was used (Gubbins, 2002; Rayment et al., 2009). Home ranges were calculated using the non-parametric utilization distribution estimators, the 95% and 50% kernel density estimators (KDE) with smoothing parameters calculated using the reference bandwidth (Rayment et al., 2009; Worton, 1989). The KDE method was chosen as it was found to perform better than other home range estimators (Kernohan, Gitzen, & Millspaugh, 2001). The 95% KDE is the estimation of the range where the animal can be found in 95% of time and is resilient to occasional visits to the areas otherwise not regularly utilized. The 50% KDE represents the core use areas (Gubbins, 2002), e.g. the area in which an animal spends 50% of its time. The home range estimates were calculated using the adehabitatHR package (Calenge, 2006) in program R (version 3.4.3; R Core Team, 2016). Since the study area comprises diverse coastline and numerous islands, all landmass was then subtracted from the estimated home ranges (Rako-Gospić et al., 2017; Silva et al., 2008). The sizes of individual home ranges, without land, and the overlap areas for each dolphin pair were calculated in km^2 using ArcGIS 10.2. software (ESRI, 2013). A matrix of overlap ratios (OLRs) for each dolphin pair was then created with the OLRs calculated as: OLR = $A_{xy}/A_x * A_{xy}/A_y$ (Silva et al., 2008), where A_{xy} is the size of an overlap area between individuals X and Y, A_x is the home range size of the individual X, and A_y is the home range size of the individual Y. Mean values and standard deviations of OLRs were calculated for each community and combinations between communities, and tested for significant differences with the Mann–Whitney test.

2.6 | Integration

The correlation between HWI and OLR matrices was tested with a Mantel's test. To visually determine if the communities were spatially segregated, the median latitude and longitude of sighting locations along with their median absolute deviation were calculated for each individual. The median value was chosen to account for sensitivity to outliers (Leys, Ley, Klein, Bernard, & Licata, 2013) and the median absolute deviation was included to represent the variability in sighting locations (Venables & Ripley, 2002). Furthermore, the 95% KDE home ranges were calculated for each community (hereafter community home range – CHR) suggested by the hierarchical cluster analysis, based on sighting locations of all individuals assigned to a community. The CHRs and median sighting locations of the individuals were plotted on the map and aligned with the dendrogram representing social structure (Figure 7).

To test how well the sample of individuals observed on 10 or more occasions represents all dolphins that regularly use the CHRs (either as residents or frequent visitors), the numbers of individuals in each community were expressed as percentage of all individuals repeatedly observed in each CHR. Individuals seen at least once annually in three or more years were considered as 'regular'.

2.7 | Movements

The results of the social structure and home range analyses suggested that the communities of individuals seen on 10 or more occasions are spatially segregated. The rates of movements within and between their CHRs were then analysed to determine the levels of interactions between them when all individuals are included, regardless of number of observations. For this analysis, the three CHRs were used as area units. For simplicity, the area units were termed according to the geographic region they fall within as: K, ND, and V (Figure 7). Sightings from the complete dataset, e.g. including all adult individuals (N = 1,024), were assigned to one of the CHR areas and used to calculate the lagged identification rates (LIRs). For movements within an area, the LIR is the probability that if the individual was observed in area A at the time *t*, it will still be in the area A at the time *tx*, where x is the time lag expressed in days. Conversely, for movements between two areas, the LIR is the probability that the individual will be seen in the area B at the time *tx* (Whitehead, 2001). To estimate the standard errors (SEs) of the LIRs, 1000 bootstrap replications were run. The best-fit movement model (see Whitehead, 2001 for details) was selected based on the lowest quasi-Akaike information criterion (QAIC) to account for over dispersion of data (Whitehead, 2007).

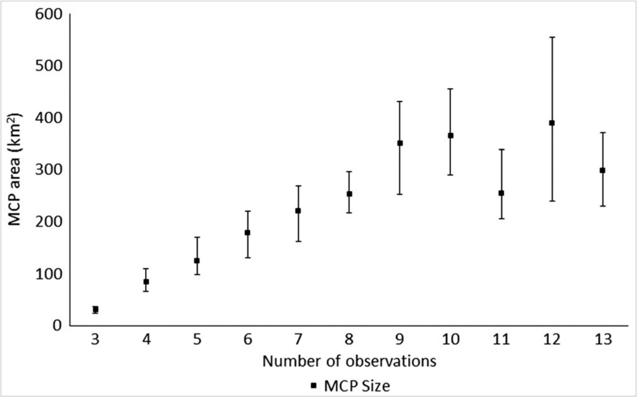

FIGURE 2 Area–observation curve with plotted mean sizes of minimum convex polygon (MCP) against number of observations per individual. The vertical bars represent standard errors

The calculated LIRs, along with SE and best-fit model were plotted against the time lag. The analysis was performed in SOCPROG 2.8 software (Whitehead, 2009).

To quantify movements between CHRs per field work season and overall, simple counts of individuals seen in more than one CHRs were made and compared to the total numbers of individuals identified in the corresponding CHRs. Furthermore, frequencies of visits to neighbouring CHRs were calculated for those individuals.

3 | RESULTS

3.1 | Survey effort and sample description

The total distance travelled on effort during the field work seasons (May–October) between 2013 and 2017 amounted to 44,171 km (Table 1). The overall effort was highest in July and lowest in October (Appendix S1). Spatial distribution and density of the effort, represented on a 4 × 4 km grid as the number of times the distance equal to cell diagonal was surveyed in each grid cell, are shown on Figure 3. During the study period, 1,122 sightings were recorded (Table 1; details in Appendix S1) from which 1,024 adult bottlenose dolphin individuals were identified. Mean number of observations per individual was 5.9 (SE = 0.23, min = 1, max = 56). The mean group size was 8.1 individuals (SE = 0.23, min = 1, max = 50). Relative encounter rates, expressed as number of groups encountered per 1 km travelled on effort, were 0.0284 (SE = 0.0032) for K, 0.0199 (SE = 0.002) for ND, and 0.0167 (SE = 0.0018) for the V study site (details in Appendix S2). These values did not differ significantly among areas (Kruskal–Wallis chi-squared = 320.73, df = 349, *P* = 0.8588).

3.2 | Social structure

Following the restriction of the dataset to individuals seen on 10 or more occasions, 177 adult individuals were included in the dataset for the social structure analysis. The average HWI for the whole population was 0.035 (SD = 0.098, coefficient of variation = 2.8). The Pearson's correlation coefficient was *r* = 0.477 (SE = 0.015), indicating that the HWI moderately represented social structure. The social differentiation was high, S = 1.062 (SE = 0.015), meaning the associations within the population were highly variable. The mean number of associations per individual was H = 139, giving the product S^2*H = 157. This value is significantly higher than 5, thus the null hypothesis of homogenous associations can be reliably rejected (Whitehead, 2008).

The hierarchical cluster analysis had the cophenetic correlation coefficient value of 0.812, indicating a good representation of the social structure (Whitehead, 2008). The population was divided into three distinct communities separated at the HWI = 0.011 level (Figure 7) where the modularity Q reached a maximum value of 0.378. One hundred and six dolphins were assigned to community K, 49 dolphins to community ND and 22 dolphins to community V, communities being named according to areas they preferentially used (Figure 7).

Existence of preferred or avoided associations was detected across whole population and within K and ND communities, but not in the V community (Table 2). There was only one pair with significantly low HWI within the whole sample, and no such pairs within single communities (Table 2).

The Mantel test showed that significantly more associations existed among individuals of the same community than among individuals assigned to different communities (*t* = 32.9, *r* = 0.49, *P* < 0.0001). Mean HWI value between individuals of K and ND communities

TABLE 1 Distances travelled on effort (in km) and number of encountered groups per year, study site and totals. Study sites: K – Kvarner, ND – North Dalmatia, V – Vis-Lastovo. Further details are given in Appendix S1

	Study site							
	K		ND		V		TOTAL	
Year	Survey effort (km)	Groups	Survey effort (km)	Groups	Survey effort (km)	Groups	Survey effort (km)	Groups
2013	2,931	90	3,245	71	869	7	**7,045**	**168**
2014	3,332	105	3,631	70	2,015	49	**8,978**	**224**
2015	3,051	96	3,329	98	4,117	110	**10,497**	**304**
2016	2,646	79	3,428	65	3,273	91	**9,347**	**235**
2017	3,487	99	2,737	54	2,080	38	**8,304**	**191**
TOTAL	**15,447**	**469**	**16,370**	**358**	**12,354**	**295**	**44,171**	**1,122**

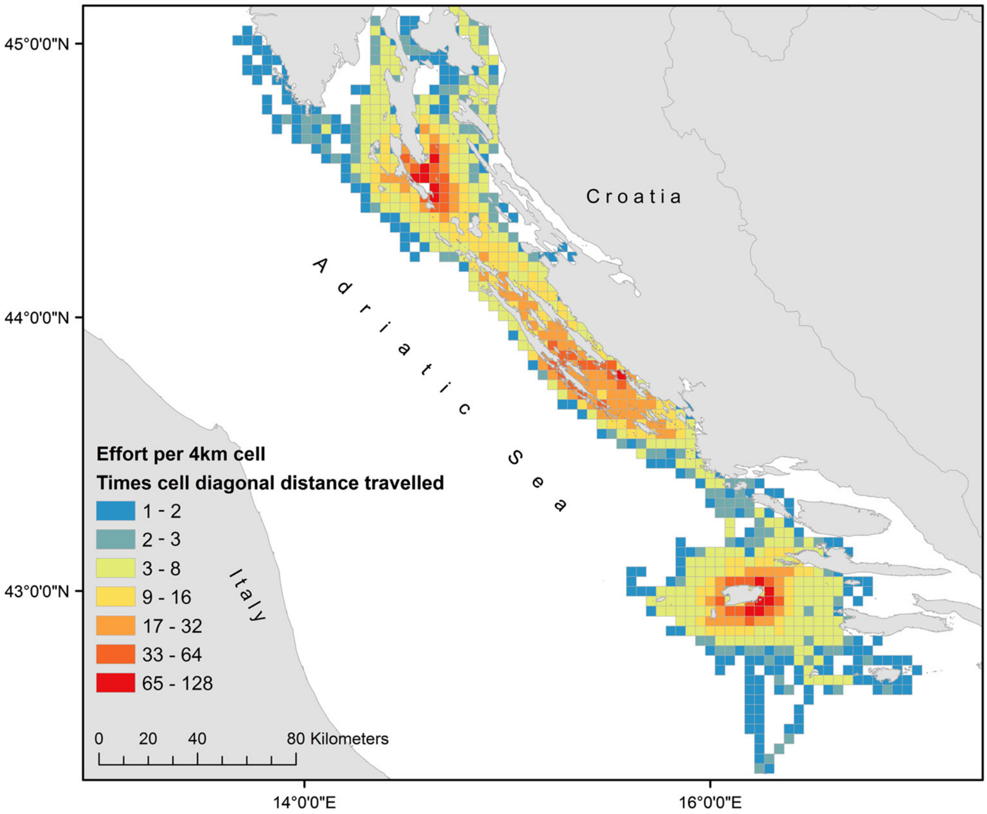

FIGURE 3 Distribution and density of effort on a 4 × 4 km grid represented as the number of times distance equal to cell diagonal was travelled within each cell

(HWI = 0.001, SD = 0.006) was significantly lower than among individuals of K community (HWI = 0.071, SD = 0.023; Mann–Whitney test, U = 9.6, *P* < 0.0001) and among individuals of ND community (HWI = 0.094, SD = 0.028; Mann–Whitney test, U = 7.8, *P* < 0.0001; Figure 4). There were no associations between individuals assigned to community V and any other community.

The network diagram (Figure 5) corresponds to findings of hierarchical cluster analysis and comparisons of HWI values within and between communities. Only 16 out of potentially 31152 meaningful associations (with HWI higher than twice the average) were found between K and ND communities, and no associations between community V and any other.

3.3 | Home ranges

The Mantel test revealed a positive correlation between both HWI and 50% KDE OLR matrices (*r* = 0.589, *P* < 0.0001), and HWI and 95% KDE OLR matrices (*r* = 0.581, *P* < 0.0001).

TABLE 2 Indices of preference or avoidance of associations in the whole sample (ALL) and within communities: K – Kvarner, ND – North Dalmatia, V – Vis. Higher standard deviation (SD) and coefficients of variation (CV) of half-weight index (HWI) in observed data than in permuted data indicate existence of preferred associations. Lower proportion of non-zero associations in observed data than in random data indicates existence of avoided associations. Number of pairs with significant HWI are shown, i.e. those with HWI higher than 97.5% or lower than 2.5% of their random association indices

	ALL		K		ND		V	
	Observed data	Permuted data	Observed data	Permuted data	Observed data	Permuted data	Observed data	Permuted data
SD (HWI)	0.09812	0.07990	0.02325	0.01553	0.02832	0.01500	0.41411	0.41672
CV (HWI)	2.80000	2.17140	0.32394	0.19804	0.29787	0.12658	0.30576	0.34863
Proportion non-zero associations	0.27080	0.32034	0.61330	0.63914	0.54422	0.56975	0.58095	0.58937
Significant pairs	234		89		21		2	
Significantly high HWI pairs	233		89		21		2	
Significantly low HWI pairs	1		0		0		0	

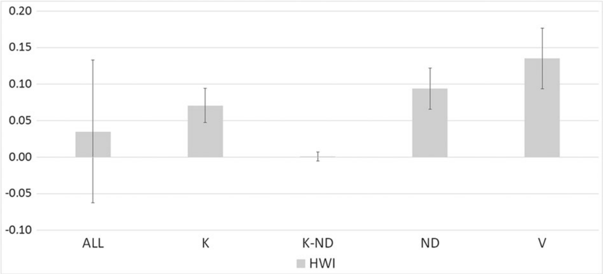

FIGURE 4 Plot of the mean half-weight index (HWI), calculated across all possible pairs (ALL), per community (K, ND, and V) and between K and ND communities. K-V and ND-V community pairs are not shown as no HWI were recorded for those pairs. Vertical bars represent standard errors. Communities: K – Kvarner, ND – North Dalmatia, V – Vis

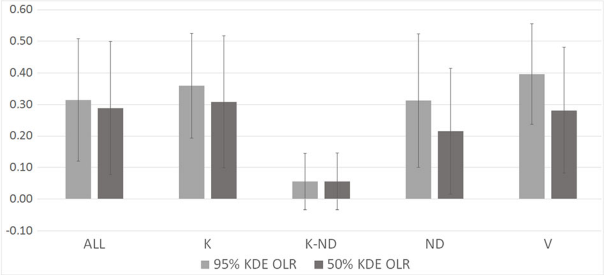

FIGURE 6 Plot of the 95% kernel density estimator overlap ratios (KDE OLRs) and 50% KDE OLRs calculated across all possible pairs (ALL), per community (K, ND and V) and between K and ND communities. K-V and ND-V community pairs are not shown as no OLRs were recorded for those pairs. Vertical bars represent standard errors. Communities: K – Kvarner, ND – North Dalmatia, V – Vis

The mean 50% KDE OLR between individuals of K and ND communities (OLR = 0.056, SD = 0.09) was significantly smaller than the mean 50% KDE OLR of individuals within the K community (OLR = 0.308, SD = 0.209; Mann–Whitney test, U = 6.367, p < 0.0001), but not significantly smaller than the mean 50% KDE OLR of individuals within the ND community (OLR = 0.215, SD = 0.199; Mann–Whitney test, U = 1.299, *P* = 0.194; Figure 6, Table 3).

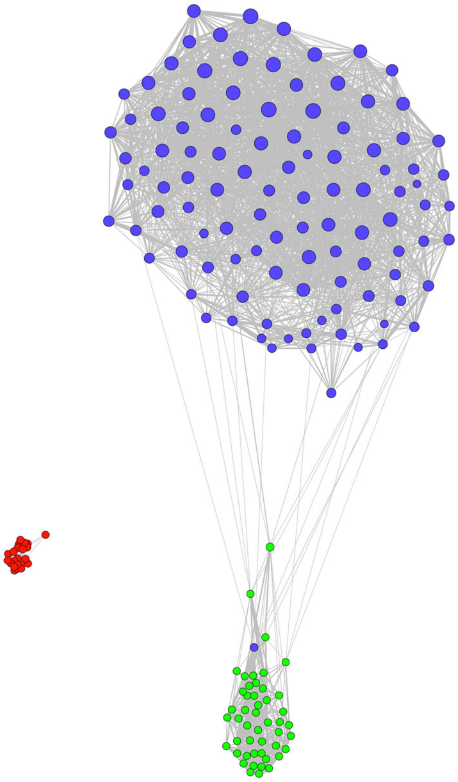

FIGURE 5 Network diagram for individuals (dots) observed on ≥10 occasions (*N* = 177). Colours represent the three discrete communities: Kvarner (K) – blue, North Dalmatia (ND) – green and Vis (V) – red. Thickness of grey lines is proportional to association strengths between individuals. Associations with half-weight index lower than double the average are excluded. Dot size is proportional to 'eigenvector centrality' of individuals

The mean 95% KDE OLR between individuals of K and ND communities (OLR = 0.056, SD = 0.089) was significantly smaller than the mean 95% KDE OLR of individuals within the K community (OLR = 0.359, SD = 0.166; Mann–Whitney test, U = 28.216, *P* < 0.0001) and within the ND community (OLR = 0.312, SD = 0.211; Mann–Whitney test, U = 12.576, *P* < 0.0001; Figure 6, Table 3).

Both the 50% KDE and the 95% KDE home ranges of individuals of V community did not overlap with individuals of either ND or K community.

The estimated 95% KDE home ranges for the three communities (CHRs) defined by the hierarchical cluster analysis, plotted on the map reveal no spatial overlap between the V and ND CHRs, and a very small overlap between K and ND CHRs (OLR = 0.000003; Figure 7). Similarly, the plotted individual median sighting locations suggest that individuals mainly range within their respective CHRs. The median absolute deviations suggest a small overlap between only a few individuals of K and ND communities, and no overlap between the individuals of ND and V communities or K and V communities (Figure 7). This is in concordance with the results on the HWI and OLRs within and between communities. The mean individual and CHR sizes are given in the Table 3.

The 106 individuals assigned to community K comprised 65% of 'regular' dolphins in their CHR; the individuals from community ND comprised 54% and from community V 23% of the 'regular' dolphins in their respective CHRs.

3.4 | Movements

The plot of the estimated lagged identification rates (LIRs) for overall movements indicates a significantly higher chance of individuals staying within the CHR area they were first observed in than moving to any other area for at least 1,000 days (Figure 8).

The plots of LIRs for movements within the three CHR areas vary from around 0.008 (K) to around 0.02 (ND). For the K and V areas, the probabilities of remaining in the area drop within the first

TABLE 3 Number of individuals assigned to each community, mean individual 50% kernel density estimators (KDE) and 95% KDE areas, 95% KDE community home ranges and overlap areas, mean half-weight index (HWI) and individual 50% KDE and 95% KDE overlap ratios (OLR) within and between communities. Communities: K – Kvarner, ND – North Dalmatia, V – Vis

	Communities					
	ALL	**K**	**K-ND**	**ND**	**ND-V**	**V**
Individuals	177	106	-	49	-	22
Mean individual 50% KDE size (km^2)	413.6	452.6	-	409.3	-	235.7
Mean individual 95% KDE size (km^2)	1,759.8	1,947.2	-	1,678.9	-	1,042.2
Community 95% KDE size (km^2)	-	2,121.5	-	1,603.0	-	1,151.9
Community HR Overlap size (km^2)	-	-	3.3	-	0	-
Mean HWI	0.0350	0.0707	0.0010	0.0938	0	0.1354
Mean individual 50% KDE OLR	0.0125	0.0128	0.0033	0.0122	0	0.0143
Mean individual 95% KDE OLR	0.0744	0.0884	0.0110	0.0626	0	0.0807

10 days and remain stable for up to around 120 days. For the ND area the probabilities of remaining in the area remain stable for up to 120 days (Figure 9). For K and V areas the model with most support from data, based on the lowest QAIC, was 'Emigration +Reimmigration+Mortality'. For the ND area, the best-fit model was 'Emigration+Mortality'.

The LIRs for movements between K and ND CHRs are significantly lower in both directions than the LIRs within either of the two areas. There seems to be a higher probability of movement from ND to K than from K to ND areas and these probabilities vary significantly with time (Figure 9). For both directions, the model with most support from data was 'Fully mixed', while the next best model with QAIC≤2 was 'Mean residence'.

The movement probabilities between ND and V CHRs were about one order of magnitude lower than those between K and ND, for both directions (Figure 9). As for the K-ND movements, for both directions the model with most support from data was 'Fully mixed', with the next best model with QAIC≤2 being 'Mean residence'.

The movement probabilities between K and V CHRs were not estimated as no individual was observed in both these areas during the study period.

Using the complete data set (1,024 adults), there were 44 movements of 37 individuals between CHR areas during the 5-year period. Of these, 43 movements of 36 individuals were between K and ND areas and one individual moved once between ND and V area (Table 4). The overall percentage of individuals moving between K

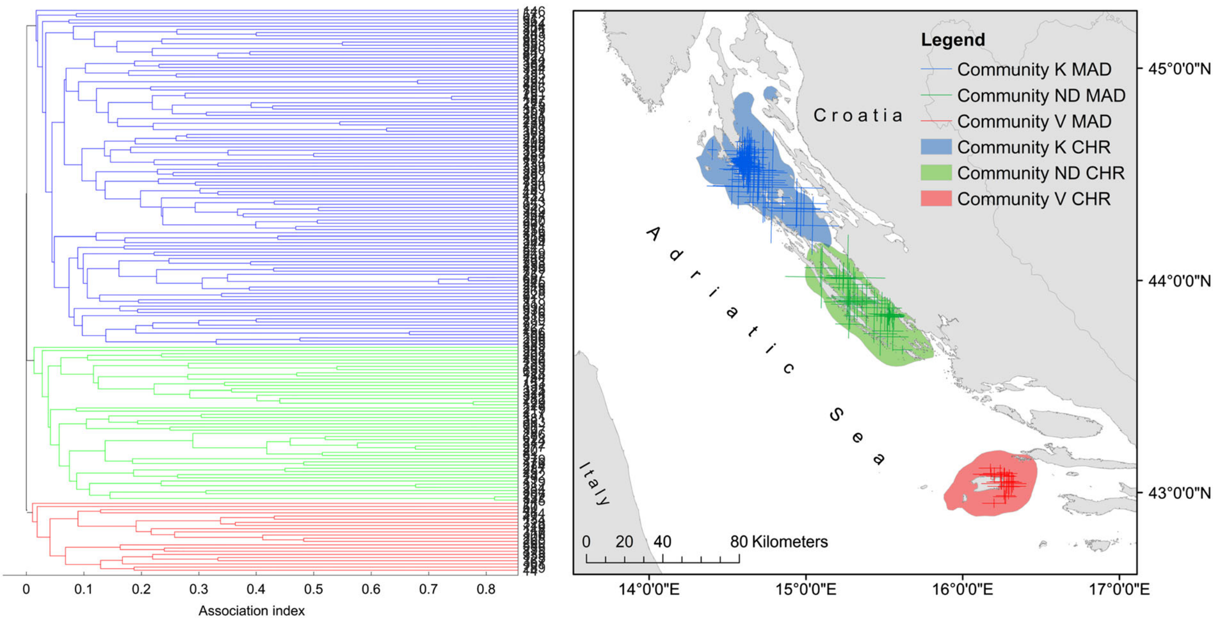

FIGURE 7 Hierarchical cluster analysis dendrogram (with cophenetic correlation coefficient of 0.812) of individuals seen on ≥10 occasions (N = 177) in the study area (on the left) with the respective 95% kernel density estimator community home ranges (CHRs), median sighting locations and median absolute deviations (MADs; on the right). Colours represent the three discrete communities: Kvarner (K) – blue, North Dalmatia (ND) – green and Vis (V) – red

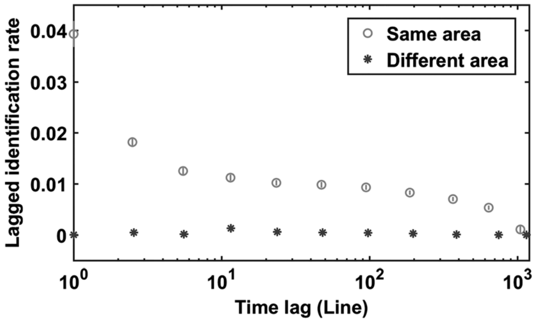

FIGURE 8 Plot of lagged identification rates indicating that within 1000 days individuals have significantly higher chance of remaining in the community home range areas (circles) than leaving the community home range areas (asterisks). The vertical bars represent standard errors obtained from bootstrap with 1000 replications

and ND areas was 3.73% of all individuals encountered in those areas, and between ND and V areas it was 0.12%. Yearly percentages varied from 0.51 to 4.93% for movements between K and ND areas and from 0 to 0.22% for movements between ND and V areas (Table 4). Of the 36 individuals observed in both the K and ND areas, 32 (88.9%) were seen in both areas in 1 year, four (11.1%) in 2 years, and one (2.8%) in 3 years. Twelve (33.3%) were females, one (2.8%) male, 5 (13.9%) probable males, and 18 (50%) of unknown sex. The one individual seen in both ND and V areas was of unknown sex.

4 | DISCUSSION

The results support the hypothesis that the common bottlenose dolphin population within the study area is structured into spatially distinct, but not completely isolated communities. The dolphins exhibited a wide range of association strengths within communities which is typical of a fission–fusion society. However, strengths of associations between the communities were consistently significantly weaker. The overlaps between home ranges of individual animals were in correlation with their association strengths, signifying that the association patterns were mirroring the ranging patterns. Analogously to the association strengths, the 95% KDE home range overlap ratios were consistently and significantly larger within communities than between them. The 95% KDE home ranges of the communities showed clear spatial separation. Only K and ND CHRs overlapped, although with an extremely low percentage (0.0003%). However, given that the distribution of survey effort was not equal across the

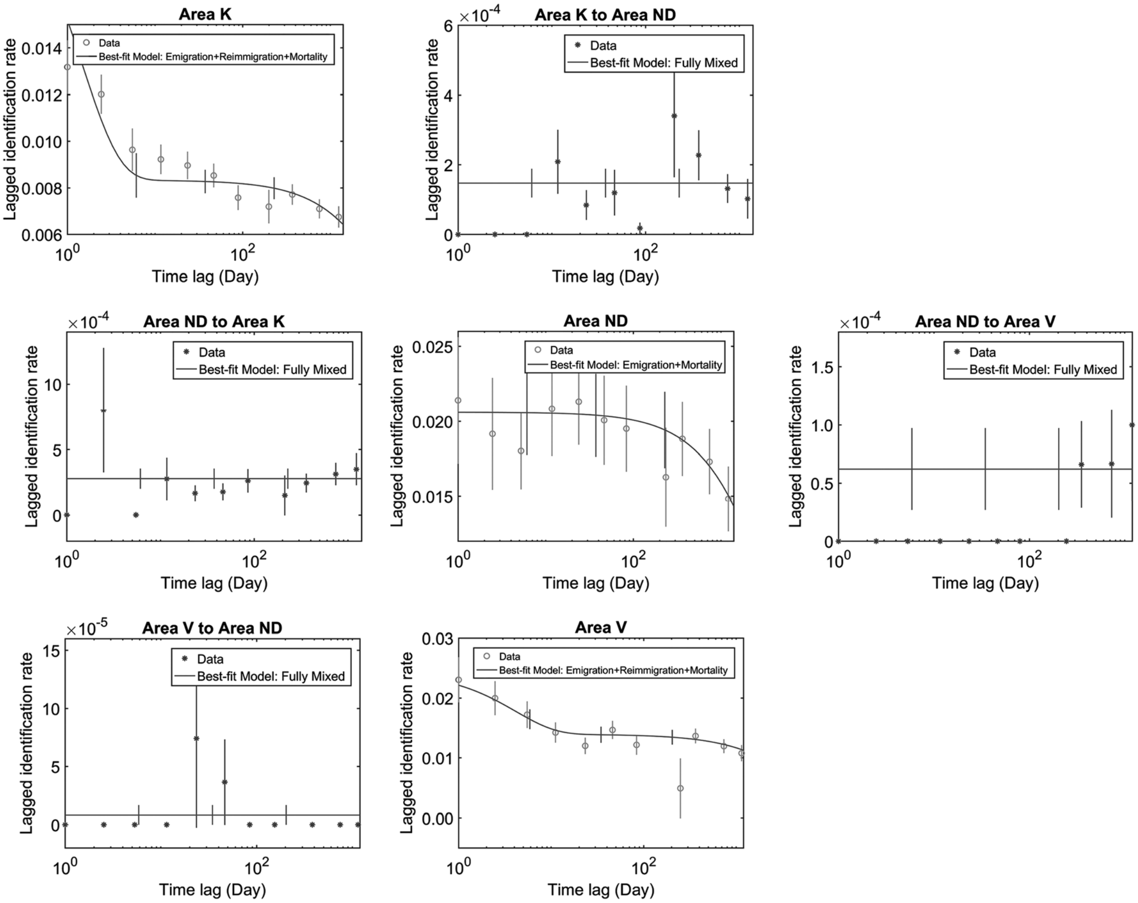

FIGURE 9 Plots of lagged identification rates (LIRs) within and between the three community home range (CHR) areas. Vertical bars represent the standard errors estimated from bootstrap with 1000 replications. The asterisks represent LIRs between and circles within CHR areas. The best-fit model for each scenario is represented with lines. LIRs between K and V CHRs were not estimated due to absence of individuals seen in both these areas. CHR areas: K – Kvarner, ND – North Dalmatia, V – Vis

TABLE 4 Movements of individuals between community home range areas, per field work season and overall, expressed as number and percentages of individuals seen in two community home range areas within the total number of individuals identified in the two community home range areas, regardless of number of observations. Communities: K – Kvarner, ND – North Dalmatia, V – Vis

	2013	2014	2015	2016	2017	2013–2017
K – ND						
Total identified	397	345	461	391	547	964
Seen in both areas (%)	3 (0.76)	17 (4.93)	13 (2.82)	2 (0.51)	8 (1.46)	36 (3.73)
ND – V						
Total identified	183	268	452	357	366	818
Seen in both areas (%)	0	0	1 (0.22)	0	0	1 (0.12)

whole study area, particularly between ND and V communities, this separation must be taken with caution (discussed below).

Different methods for delineating social entities exist. The choice of the appropriate method depends on the kind of social entity one is trying to describe (community, group, or social unit), while the choice of the threshold value separating the social entities depends on the level of structuring one is interested in (Whitehead, 2008). Similarly, the minimum number of observations needed to estimate the home range is a subject of debate (Titcomb, O'Corry-Crowe, Hartel, & Mazzoil, 2015). Seaman et al. (1999) suggest a minimum of 30 observations to obtain precise estimates. In the present study, the aim was to test whether there was a general social and spatial division into communities along the whole study area, without looking into the fine-scale structuring and precise ranging patterns within the communities. Thus, a relaxed criterion of 10 observations per individual was used (as suggested by the area–observation curve, Figure 2) to prevent underestimation of home ranges while maximizing the sample size. With this sample, the HWI value at which the communities were delineated was quite low (0.011), but this was expected given the generally weak association strengths reported for bottlenose dolphins (Augusto, Rachinas-Lopes, & dos Santos, 2012). Also, the cophenetic correlation coefficient was >0.8 and the modularity was >0.3, which suggests a good power for delineating the communities (Bridge, 1993; Newman, 2004). This division produced communities in which association patterns were positively correlated with the individual home range overlaps. Therefore, we consider the use of individuals seen on 10 or more occasions a viable trade-off between accuracy of the home range estimates and the need to maintain sample size large enough to represent the communities.

However, the restriction of sample to individuals seen on 10 or more occasions yielded different levels of representation of all 'regular' dolphins in the three areas. Individuals assigned to K and ND communities comprised >50% of all 'regular' dolphins (seen in 3 or more years) in those areas. However, those assigned to V community comprised only 23% of dolphins considered as 'regular' in the V area, limiting the ability to infer generalizations from a small sample for the V

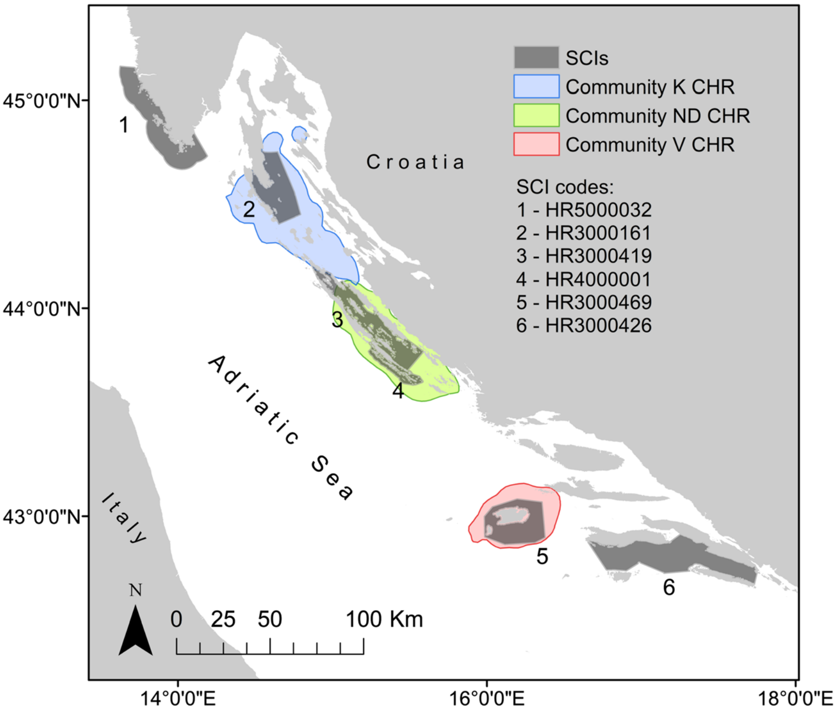

FIGURE 10 Sites of Community Importance (SCIs) for bottlenose dolphins within the Croatian Adriatic Sea in relation to the three community home ranges (CHRs; 95% kernel density estimator). Details on SCIs are available at: http://natura2000.eea.europa.eu/. Communities: K – Kvarner, ND – North Dalmatia, V – Vis

area. Habitat characteristics may influence residency. Shallower coastal habitats generally have spatially and temporally predictable food resources, promoting long term residency of dolphins to smaller areas, while deeper offshore habitats with unpredictable resources induce wide-ranging behaviour and thus lower residency in certain areas (Gowans, Würsig, & Karczmarski, 2008). Consequently, the probability to re-encounter an individual a sufficient number of times, given the similar survey effort, would be higher in coastal areas. In this sense, the shallow, coastal waters of the K and ND areas would explain larger proportion of 'regular' individuals (36% of all identified individuals for both areas) and consequently larger number of individuals satisfying the 10 observations criterion. Conversely, the V area is predominantly an open habitat with characteristics that promote lower site-fidelity: average water depths >100 m, prevalence of uniform physio-geographic features and depleted demersal fish stocks (Holcer, 2012). This is also reflected in relative encounter rates, which were lower in the V region compared to the other two study sites, although not significantly. Accordingly, the proportion of 'regulars' within all encountered individuals in the V area was lower (25%; $N = 94$), and consistent with earlier study in the same area when 109 out of the estimated 400 individuals (27%) were classed as 'regulars' (Holcer, 2012). The resulting low proportion of dolphins satisfying the 10 observations criterion requires further work with spatially extended survey effort to provide more robust description of the community in the V region.

The mean HWI association rates of the three identified communities (K HWI = 0.07, ND HWI = 0.09, V HWI = 0.13) were generally similar to those described in other studies, which range from as low as 0.01 in the Indian River Lagoon (Titcomb et al., 2015) to as high as 0.5 in the Brittany region, east Atlantic (Louis et al., 2017). The individuals in the K community had more associations but with lower strength, whereas those in ND and V communities had fewer but stronger associations. This may be explained by demographic characteristics (Lehmann & Boesch, 2004) and isolation due to geographic barriers (Lusseau et al., 2003). In small communities, individuals interact more often with fewer community members. In accordance with this, the three communities with the highest reported mean HWI values, in the Sado estuary, Portugal (Augusto et al., 2012), Doubtful Sound, New Zealand (Lusseau et al., 2003) and around Sein Island, France (Louis et al., 2017), are relatively small, counting less than 100 individuals, and resident. Contrary to this, Daura-Jorge, Cantor, Ingram, Lusseau, and Simões-Lopes (2012) report on a resident community in Laguna (Brasil), counting 35 individuals, but with the comparatively low mean HWI value of 0.05. Furthermore, the aforementioned communities inhabit different habitat types. Doubtful Sound, Sado estuary, and Laguna are relatively enclosed bodies of water, whereas Sein Island is a relatively open habitat at the shelf edge, similar to the V area in this study. Thus, the number and strength of the associations within a community cannot be explained solely by its size or geographic isolation.

The division into distinct communities despite the absence of physical barriers and at a relatively small geographical scale is not unique. Various levels of social and spatial segregation are described, ranging from those where communities are both socially and spatially segregated (Titcomb et al., 2015; Urian et al., 2009) to those where communities retain social segregation despite the considerable home range overlap (Chilvers & Corkeron, 2001; Genov et al., 2019; Lusseau et al., 2006). In the present study, these communities exhibited both the social and spatial segregation. The K and ND communities inhabit areas adjacent to each other while maintaining low levels of interactions. While there is some overlap between their home ranges, albeit extremely small, the median sighting locations show that the individuals range mainly centrally within their respective community home ranges. Thus, the bordering areas of the K and ND communities' home ranges possibly represent the extremes to which the community members range, which would be in accordance with the relatively low observed number and infrequent nature of movements between them.

The distinct separation of the V community was clear, with no overlap with the ND community based on both the association indices and the home range overlap analyses. However, this separation could be the artefact of low survey effort between the ND and V areas (Figure 3). This leaves space for at least three scenarios: there may be a clear border between the ND and V communities somewhere within this 'gap' area, there may be no clear border, but rather a substantial spatial overlap between the two communities, or another distinct community may exist in this area. However, the analysis of movements between areas, which included all adults regardless of number of observations, i.e. also those excluded from the HWI and OLR analyses, revealed only one individual seen in both ND and V areas during the study period. Aerial surveys of the summer distribution of bottlenose dolphins in the Adriatic revealed their preference for areas with water depths <100 m (Fortuna et al., 2018). The minimum distance between the borders of the ND and V community home ranges is 55 km and this area coincides with water depths >100 m (Figure 1), which may present a natural barrier and explain low interactions between ND and V communities observed in this study. Further studies with increased effort in the 'gap' area are needed to better determine the borders and interaction rates between the ND and V communities.

The observed social and spatial organization of the bottlenose dolphins is likely to be a result of both intrinsic and extrinsic factors. Similar to others, results from this study show existence of preferred and avoided associations which can arise from differences in social behaviour and the resulting ranging patterns depending on the age, sex, and kinship. For instance, natal philopatry was described in the K region where the home ranges of former calves considerably overlap with their natal home ranges and those of their mothers (Rako-Gospić et al., 2017). The same study showed that the ranging patterns varied primarily in relation to sex and reflected the reactions of males and females to fisheries and nautical tourism, two primary stressors in the K region (Fortuna, 2006; Mackelworth, Holcer, & Fortuna, 2013).

The spatial or social aspects of population structure can change over time as a response to environmental changes. For instance, in Moreton Bay, Australia, two communities with overlapping home ranges, but socially segregated based on utilization of different foraging techniques ('trawlers' and 'non-trawlers') lost their distinct association patterns and started interacting after the significant reduction in commercial trawling (Ansmann et al., 2012). In the present study, pooled data from the five summer seasons were used when the survey effort was concurrently conducted across the whole study area. Restricting the dataset to single summer seasons would have further reduced the number of individuals with a sufficient number of observations below a meaningful level. It is therefore impossible to infer temporal changes between or within years, but the results should rather be considered as a 'snapshot' of the 5-year period. However, the comparisons of the reference dorsal fin catalogues from earlier years showed similar limited movements between areas identified in this study as distinct community home ranges (Holcer, 2012; Pleslić et al., 2015). It could therefore be argued that the spatial population structure remains stable across for at least a decade.

The analysis of LIRs revealed a generally higher probability of individuals being re-sighted within the same area than in an adjacent area. This is consistent with the findings of the association indices and home range overlap analyses within and between communities. The best-fit models for movements within areas for all three communities included emigration and mortality, and additionally reimmigration for the K and V communities. This suggests that the communities are not completely isolated. Furthermore, given the duration of the study (5 years) some mortality would also be expected, as suggested by the best-fit model for all three communities. In fact, one individual belonging to the ND community was found dead in 2017. However, given that stranding events were not systematically recorded, the actual mortality rates cannot be inferred.

The analysis of movements between the community home range areas further corroborates the relative isolation of communities, despite the absence of physical barriers. The overall number of individuals observed in more than one CHR area was generally low compared to total number of individuals identified in those areas. As expected, the movements between CHR areas seem to be inversely related to distance between them, as most individuals moved between the adjacent K and ND areas, and only one between the ND and V area, which are 55 km apart. Low movement rates between distant areas were also reported in the Black Sea where only three out of the 350 identified individuals were resighted during 3 years in different study sites as far as 325 km apart (Gladilina et al., 2016). Similar occasional long-distance movements were recorded elsewhere: several 100 km in Texas, USA (Würsig, 2017), up to 265 km in Greece (Bearzi, Bonizzoni, & Gonzalvo, 2011), up to 427 km in Ligurian Sea (Gnone et al., 2011) and 130 km in northern Adriatic Sea (Genov et al., 2016). In contrast to this, Thompson et al. (2011) report on a regular high movement rate between three study sites along the eastern Scottish coast (tens of km apart). In this study, most of the movements of individuals (88.9%) between CHR areas were recorded only in 1 year. Thus, the majority of those movements could be characterized as occasional sallies to neighbouring areas rather than regular occurrences. Nevertheless, those wide ranging individuals, although their proportion within a population may be small, play an important role as they can result in gene flow (Gaspari et al., 2015) and disease transfer between communities (Carnabuci et al., 2016). In the K region, females have larger home ranges than males (Rako-Gospić et al., 2017). This is in concordance with Gaspari, Holcer, et al. (2015) who found that, in the Adriatic Sea, the females are the principal gene flow mediators. However, in the present study sex bias in movements could not be inferred as only 13 out of 36 individuals seen in two CHR were of known sex.

The results of this study extend the understanding of the bottlenose dolphin population structure within the Croatian Adriatic Sea and provide a baseline for further research and monitoring to support conservation initiatives. The home ranges of the three identified communities generally overlap with the four out of six SCIs for bottlenose dolphins currently declared within the Croatian Adriatic Sea (Figure 10). The Cres and Lošinj SCI (HR3000161) and the V SCI (HR3000469) lie completely within the home ranges of the K and V communities and cover 24.7% and 45.1% of their home ranges, respectively. The ND community overlaps with two SCIs (HR3000419 and HR4000001), which together represent 44% of its home range. Within these areas, as elsewhere in the Mediterranean, overfishing, boat disturbance, and underwater noise pollution are among the main threats to bottlenose dolphins (Bearzi, Fortuna, & Reeves, 2008; Rako et al., 2013; Rako, Picciulin, Vilibić, & Fortuna, 2012). However, there are differences in the temporal and spatial distribution, and intensity of these threats. For instance, bottom-trawling is common in the V area (Holcer, 2012) and K region where it also shows seasonal variations (Rako et al., 2013), whereas it is rare in the ND (*own data*). There are no aquaculture sites in the V region, two in the K region and 11 ND where frequency of entanglements in fishing gear is also the highest (*own data*). Thus, once these SCIs are declared as SACs, conservation measures will need to address the site-specific effects of fisheries and aquaculture on the local communities to comply with the Habitats Directive (Council Directive 92/43/EEC). While the baseline data for the K and V communities exist (Holcer, 2012; Pleslić et al., 2015; Rako-Gospić et al., 2017), studies on demographic parameters, fine-scale social structure and habitat use for the ND community is required. The results presented here can be used as sampling units or covariates in those studies to increase their accuracy. These would provide a basis for monitoring of negative interactions with fisheries and aquaculture (mortality due to by-catch and entanglements in fishing gear) to identify how they reflect on the wellbeing of the local communities and to support mitigation measures.

Furthermore, to maximize the protection of the bottlenose dolphins within the Adriatic, the expansion of biological research effort is recommended to address the currently data deficient areas of the other two SCIs (Western Istria (HR5000032) and Lastovo Channel (HR3000426), Figure 10) and the 'gap' between the ND and V areas. Spatial expansion of research should be coupled with photo-identification data sharing among all research groups in the Adriatic Sea to enable detection of long-range migrations (if any) and their effects on the connectivity and demographics of the local communities. A broad-scale biopsy campaign should be undertaken to corroborate the photo-identification data. Such a campaign can provide knowledge on toxicological burden imposed on the local communities and its effects on their viability. Furthermore, it would allow a fine-scale detection of the genetic connectivity between the coastal communities or influx from pelagic populations as a potentially important source of genetic variability (Gaspari, Scheinin, et al., 2015). Such information can further clarify the movement rates between the communities found in this study and thus help to integrate the management of the SCIs. For example, protection of corridors between community home ranges can be introduced where needed, to ensure genetic continuity between them.

Many of the SCIs for bottlenose dolphins comprise coastal habitats that are undergoing dynamic development associated with tourism, fisheries, and maritime traffic. The Habitats Directive requires that any development plan with a potential impact on SCIs must be assessed in respect to conservation objectives of the site (Council Directive 92/43/EEC, 11). This has significant implications for the Republic of Croatia, which who is required to maintain the favourable conservation status of this species in, at least, the sites designated for their conservation. Combining biological data with human-use patterns within the current SCIs will provide information on the different levels of threats along the eastern Adriatic coast. Within broader maritime spatial planning, the decision support tools, such as Marxan or Zonation, can combine the results of this study with the socio-economic data to examine optimal size and placement of the SCIs and potentially corridors between them, to relieve threats to the individual bottlenose dolphin communities throughout their range.

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SUPPORTING INFORMATION

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Supplementary material for manuscript

Social structure and spatial distribution of bottlenose dolphins (*Tursiops truncatus*) along the Croatian Adriatic coast

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S1. Distributions of survey effort and dolphin group encounters per month, year, study site and totals

Table S1. Distances travelled on effort (in km) per month, year, study site and totals

Year	Study site	May	June	July	August	September	October	
2013	L	247	539	701	412	832	200	**2931**
	ND	0	581	944	794	926	0	**3245**
	V	278	121	147	323	0	0	**869**
Annual total		525	1241	1792	1529	1758	200	**7045**
2014	L	461	478	609	787	597	400	**3332**
	ND	0	760	1012	996	657	206	**3631**
	V	0	0	705	985	325	0	**2015**
Annual total		461	1238	2326	2768	1579	606	**8978**
2015	L	531	802	922	500	225	71	**3051**
	ND	80	610	1209	1211	149	70	**3329**
	V	678	1303	1312	628	196	0	**4117**
Annual total		1289	2715	3443	2339	570	141	**10497**
2016	L	579	649	457	475	430	56	**2646**
	ND	0	679	981	1048	665	55	**3428**
	V	633	1022	1064	554	0	0	**3273**
Annual total		1212	2350	2502	2077	1095	111	**9347**
2017	L	514	643	849	887	471	123	**3487**
	ND	410	826	562	722	87	130	**2737**
	V	0	683	592	713	92	0	**2080**
Annual total		924	2152	2003	2322	650	253	**8304**
TOTAL		**4411**	**9696**	**12066**	**11035**	**5652**	**1311**	**44171**

Table S2. Time spent on effort (in decimal hours) per month, year, study site and totals

Year	Study site	May	June	July	August	September	October	**TOTAL**
2013	L	22,05	25,52	35,03	23,03	36,42	8,57	**150,62**
	ND	0	25,47	40,98	39,92	36,33	0	**142,7**
	V	13,23	5,25	5,98	14,78	0	0	**39,24**
Annual total		35,28	56,24	81,99	77,73	72,75	8,57	**332,56**
2014	L	20,4	19,92	24,52	33,08	25,55	16,77	**140,24**
	ND	0	31,28	44,7	44,83	25,47	9,9	**156,18**
	V	0	0	25,48	45,45	15,75	0	**86,68**
Annual total		20,4	51,2	94,7	123,36	66,77	26,67	**383,1**
2015	L	23,48	33,37	28,3	18,28	9,75	5,6	**118,78**
	ND	2,87	21,73	51,47	48,85	5,3	2,67	**132,89**
	V	27,97	53,22	60,5	27,23	7,82	0	**176,74**
Annual total		54,32	108,32	140,27	94,36	22,87	8,27	**428,41**
2016	L	20,15	25,15	18,7	18,9	17,83	4,62	**105,35**
	ND	0	23,3	39,63	40,72	25,52	7,68	**136,85**
	V	28,03	44,65	42,65	24,63	0	0	**139,96**
Annual total		48,18	93,1	100,98	84,25	43,35	12,3	**382,16**
2017	L	21,12	27,6	36,37	37,62	19,52	10,13	**152,36**
	ND	15,32	31,45	22,72	27,8	3,78	5,47	**106,54**
	V	0	24,77	23,35	27,77	2,85	0	**78,74**
Annual total		36,44	83,82	82,44	93,19	26,15	15,6	**337,64**
TOTAL		**194,62**	**392,68**	**500,38**	**472,89**	**231,89**	**71,41**	**1863,87**

Table S3. Numbers of encountered groups per month, year, study site and totals

Year	Study site	May	June	July	August	September	October	**TOTAL**
2013	L	15	11	20	23	17	4	**90**
	ND	0	14	18	19	20	0	**71**
	V	5	0	0	2	0	0	**7**
Annual total		20	25	38	44	37	4	**168**
2014	L	16	15	19	19	15	21	**105**
	ND	0	18	25	16	8	3	**70**
	V	0	0	16	25	8	0	**49**
Annual total		16	33	60	60	31	24	**224**
2015	L	11	16	32	26	6	5	**96**
	ND	3	6	41	41	7	0	**98**
	V	19	29	44	11	7	0	**110**
Annual total		33	51	117	78	20	5	**304**
2016	L	13	14	20	19	10	3	**79**
	ND	0	8	19	20	16	2	**65**
	V	21	18	34	18	0	0	**91**
Annual total		34	40	73	57	26	5	**235**
2017	L	12	21	25	21	11	9	**99**
	ND	15	10	8	20	1	0	**54**
	V	0	11	12	11	4	0	**38**
Annual total		27	42	45	52	16	9	**191**
TOTAL		**130**	**191**	**333**	**291**	**130**	**47**	**1122**

Table S4. Time spent during group encounters (in decimal hours) per month, year, study site and totals

Year	Study site	May	June	July	August	September	October	**TOTAL**
2013	L	14,78	11,33	25,47	22,37	16,03	3,08	**93,06**
	ND	0,00	9,82	10,78	12,80	9,65	0,00	**43,05**
	V	5,22	0,00	0	2,65	0	0,00	**7,87**
Annual total		20	21,15	36,25	37,82	25,68	3,08	**143,98**
2014	L	8,95	8,98	11,42	10,95	14,62	14,70	**69,62**
	ND	0,00	9,47	10,40	8,62	2,73	0,52	**31,74**
	V	0,00	0,00	15,82	16,58	4,67	0,00	**37,07**
Annual total		8,95	18,45	37,64	36,15	22,02	15,22	**138,43**
2015	L	11,07	10,62	17,52	23,45	2,62	2,65	**67,93**
	ND	0,48	2,83	14,68	14,63	2,53	0,00	**35,15**
	V	12,13	31,38	33,65	7,18	5,02	0,00	**89,36**
Annual total		23,68	44,83	65,85	45,26	10,17	2,65	**192,44**
2016	L	6,60	11,18	14,65	19,40	6,22	3,17	**61,22**
	ND	0,00	2,18	7,93	7,83	5,60	1,18	**24,72**
	V	12,87	13,57	24,00	17,85	0,00	0,00	**68,29**
Annual total		19,47	26,93	46,58	45,08	11,82	4,35	**154,23**
2017	L	8,97	13,73	23,23	19,93	8,53	8,40	**82,79**
	ND	2,92	1,82	3,63	5,53	0,30	0,00	**14,2**
	V	0,00	7,18	11,03	11,27	4,25	0,00	**33,73**
Annual total		11,89	22,73	37,89	36,73	13,08	8,4	**130,72**
TOTAL		**83,99**	**134,09**	**224,21**	**201,04**	**82,77**	**33,7**	**759,8**

S2. Encounter rates

To determine if significant differences in bottlenose dolphin occurrence exist between the study sites, relative encounter rates were calculated. The study area was overlaid with a 4 x 4 km grid and for each grid cell total distance travelled on effort (L), number of groups (*n*) and proportion of the sea (*s*) were calculated. Cells with L< 5.66 km (cell diagonal length) were excluded from analysis to reduce bias from insufficiently surveyed cells. The relative encounter rates (ER) were calculated for the remaining cells as ER=*n*/L and corrected for the proportion of the sea by multiplying with *s*. The overall encounter rates were obtained for each study site by averaging ER values from the cells that lay within the respective study site (Figure S1, Table S5). Relative encounter rates did not differ significantly among areas (Kruskal-Wallis chi-squared = 320.73, df = 349, p-value = 0.8588)

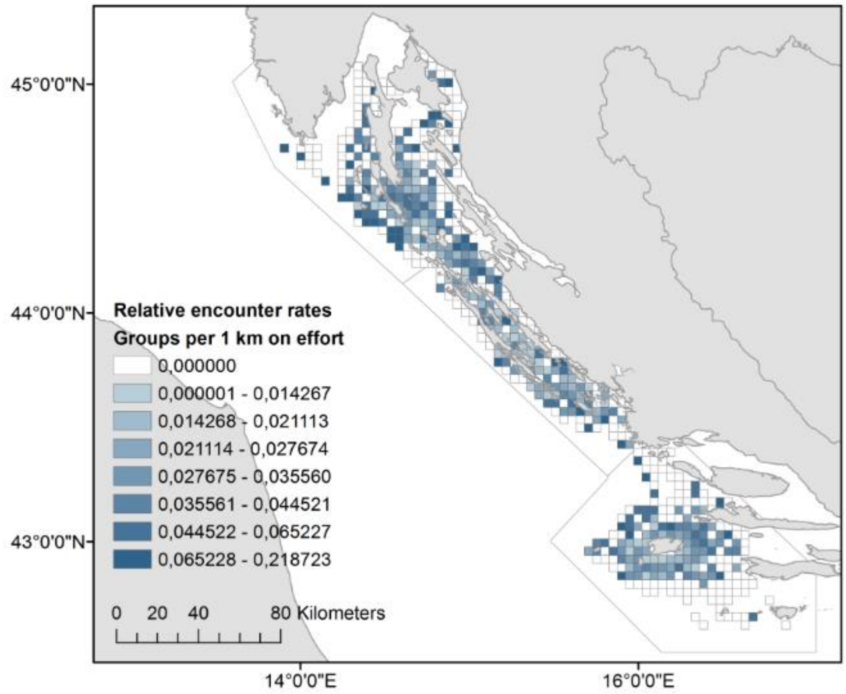

Figure S1. Relative encounter rates expressed as number of groups encountered per 1 km travelled on effort. Cells in which total distance travelled on effort less than the cell diagonal are not shown

Table S5. Relative encounter rates per study area. SE – standard error.

Study area	L	ND	V
Mean ER (groups/100 km)	2.84	1.99	1.67
SE	0.32	0.20	0.18

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Factor associated variations in the home range of a resident Adriatic common bottlenose dolphin population

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ABSTRACT

This study investigates the influence of the most dominant factors (association patterns, gender, natal philopatry and anthropogenic pressure) on the home range size of the 44 most resident common bottlenose dolphins (*Tursiops truncatus*) inhabiting the waters of the Cres-Lošinj archipelago (north Adriatic Sea, Croatia), a recently declared NATURA 2000 SCI. Results show that variations in home range patterns (MCP, 95% KDE and 50% KDE home range size) among the individual resident dolphins are primarily related to differences in gender and reflect the way in which different genders respond to external stressors. In addition, results confirm the seasonal influence of nautical tourism on both female and male dolphins through changes in their home range sizes. The overall results improve current knowledge of the main anthropogenic threats that should be taken into consideration when developing conservation measures to be applied to this Cres and Lošinj SCI.

1. Introduction

The common bottlenose dolphin (*Tursiops truncatus*) is a cosmopolitan cetacean species with its presence being reported for all temperate and tropical seas (Reeves et al., 2002). In the Adriatic Sea, the presence of local populations inhabiting mainly coastal areas has been confirmed (Genov et al., 2008; Fortuna, 2006; Holcer, 2012; Pleslić et al., 2015; Gaspari et al., 2015). Photo-identification data since 1995 has revealed that the coastal waters of the Cres-Lošinj archipelago (north Adriatic Sea, Croatia) are home to about 200 common bottlenose dolphins (Bearzi et al., 1997; Pleslić et al., 2015). This population is characterised as relatively closed with a low degree of individual displacement to significantly distant areas, and with movements that appear to be strongly habitat dependant (Fortuna, 2006; Genov et al., 2008; Pleslić et al., 2015). High sighting frequency and regular re-sightings of known individual dolphins indicate their long-term fidelity to this specific region. Due to its importance as a habitat for this resident common bottlenose dolphin population, the Cres-Lošinj area was designated as a Site of Community Importance (SCI), part of the European Union NATURA 2000 ecological network (Cres and Lošinj SCI, HR3000161), in December 2014. This is in accordance with the European Habitat Directive (Council Directive 92/43/EEC) that listed *Tursiops truncatus* in Annex II requiring all the EU member states to establish Special Areas of Conservation where populations are resident. Furthermore, according to the article 6 of this Directive, each SCI must be designated a Special Area of Conservation (SAC) within six years, with associated conservation regime corresponding to the ecological requirements of the site.

In order to achieve the preservation of this important habitat of common bottlenose dolphins and therefore to contribute to their conservation it is crucial to identify the resident dolphins' home range. The home range represents a defined area in which an animal lives (Burt, 1943). It is an important ecological feature, which indicates the space required for an individual animal to fulfil its everyday activities. Home ranges may vary between and within species, and can depend on gender, age or season (Burt, 1943; Connor, 2000; Wells et al., 1980). It generally encompasses areas of higher usage as well as those less visited by the animals (Sprogis et al., 2016). Home range size depends on the biological requirements of the individual and is influenced by physical characteristics of the host habitat (topographic features) and the biological components such as the availability of mates for reproduction, the availability of food resources and protection from predators (Ballance, 1992; Defran et al., 1999; Martinez-Serrano et al., 2011; McNab, 1963).

Many marine mammals are capable of travelling very long distances. However, individuals within some populations may remain resident in relatively small areas (Bjørge, 2001). Although these individuals generally have well defined home ranges, their distribution

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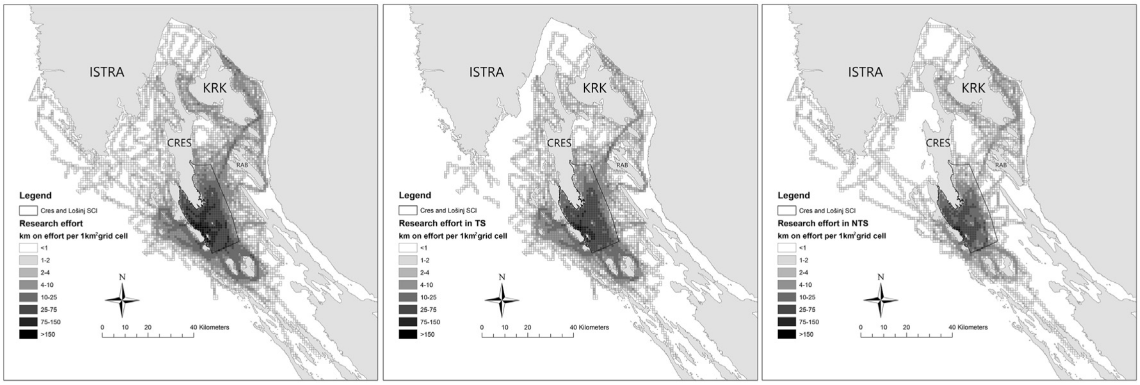

Fig. 1. Study area and Cres and Lošinj SCI. Yearly and seasonal research effort is presented in colour scale corresponding to the length in km surveyed within 1 km^2 grid cells.

and the use of space within these home ranges refer to the individual movements rather than to an entire population (Morales et al., 2010). This is particularly true in fission-fusion societies, such as those seen in many dolphin species, where individuals within the same population may have greatly different ranging patterns (Defran et al., 1999) and individuals may alternate between local site-fidelity and longer ventures away from the site of their first identification (Bearzi et al., 1997; Genov et al., 2016).

Previous studies on the behavioural ecology of common bottlenose dolphins (*Tursiops truncatus*, Montagu 1821) have revealed a great variability in their home range characteristics (Connor et al., 2000; Defran et al., 1999; Wells et al., 1999) that may be due to habitat heterogeneity or to differences in the use of space between the genders (Connor, 2000; Wells et al., 1980). As dolphins are social animals, association patterns among individuals, as well as their kinship, may also influence their space use and ranging patterns (Frère et al., 2010). In fact, home range overlap between the individuals may often provide indirect information on the social bonds between them (Carter et al., 2009; Frère et al., 2010).

In many cases, variations in home range patterns between dolphins may be associated to external perturbations and reflect a change in the quality or availability of their preferred habitats. In coastal areas, subject to intense human exploitation, changes in home range size and habitat use may be particularly frequent (Bejder et al., 2006; Fortuna, 2006; Jensen et al., 2009; Rako et al., 2013a).

In the Adriatic Sea dolphins lack natural predators due to the reduced presence of large shark species (De Maddalena and Heim, 2012; Jukić-Peladić, 2001). The main threat they face is intense human use of their ecosystem, particularly related to fishing and seasonal tourism, the two dominant human activities within the Cres–Lošinj area (Mackelworth et al., 2003; Fortuna, 2006).

The local fishery within the study area consists mainly of the small bottom trawlers ($<$ 12 m) and gillnetters active in the area throughout the whole year, with number on trawlers being higher during the winter months (Rako et al., 2013b). Previous studies within this area have found a positive correlation between the trawling locations and the presence of dolphins (Bearzi et al., 1999; Zekan, 2011). This is due to both, opportunistic feeding by dolphins on the concentrated food source represented by a bottom trawling net and overlap of feeding and fishing grounds. Feeding behind trawlers is a strategy energetically less demanding in comparison to other feeding strategies that require searching and capturing of the prey (Fortuna et al., 1996).

Adversely, activities related to tourism are seasonal; in particular, there is a substantial increase in the number of recreational boats using this area during the summer months (Fortuna, 2006; Rako et al., 2013b). This has affected the bottlenose dolphin distribution and habitat use in the region (Fortuna, 2006; Rako et al., 2013a). There is an estimated increase of 350% in the number of short-term moorings in the summer months (Lošinj Y/C Marina LP-turizam d.o.o. and Marina Lošinj *Morus alba* d.o.o., pers. comm., 24 November 2016). Intense leisure boating has already proven to have an impact on the distribution and acoustic communication of residents of this dolphin population (Rako et al., 2013a; Rako-Gospić and Picciulin, 2016).

Based on 10 years of photo-identification data, this paper assesses the home range characteristics of the 44 most resident bottlenose dolphins in the Cres-Lošinj population. It evaluates the influence of the most dominant factors, association patterns, gender, natal philopatry and anthropogenic pressure, on the size of their home range. The results provide a better understanding of ranging patterns of these resident bottlenose dolphins and identify the main anthropogenic threats that should be taken into consideration when developing conservation measures to be applied to this Cres and Lošinj SCI.

2. Materials and methods

The home range estimates of individual bottlenose dolphins were based on photo-identification surveys carried out in the Cres-Lošinj archipelago (northern Adriatic Sea, Fig. 1) between 2005 and 2014. Daily surveys were conducted using a 5.8 m RIB powered by a four-stroke 90 HP outboard engine, in favourable sea conditions (sea state $\leq$ 2 Beaufort scale and visibility not obscured by haze, fog or rain) at a speed of about 15 knots. The research area (Fig. 1) extends over approximately 2000 km^2 and includes Cres-Lošinj SCI (HR3000161). It is characterised by numerous islands and islets, steep rocky shores and a seabed patched with muddy areas and sea grass flats. The average sea depth is about 70 m (Arko-Pijevac et al., 2003).

Photo-identification surveys were conducted throughout the year, although research effort was most intense between May and September due to the adverse weather conditions in the winter months (Fig. 1). The photo-identification protocol is described in detail by Pleslić et al. (2015). To account for the unevenly distributed research effort and to test whether it may have affected the frequency of sightings of individual dolphins, collected data were normalized by calculating individual dolphin encounter rates (ER; Bearzi et al., 2005; Fortuna, 2006; Rako et al., 2013a). These ERs were calculated as n_i/L, where n_i is the overall or seasonal number of individual dolphin encounters and L is the length in kilometers of the overall or seasonal survey effort. The yearly and seasonal effort and ER of individual dolphins are presented in Table 2.

In order to achieve the independence of the home range calculations from the sampling size, the increased sampling rates are highly recommended as it improves home range estimates (Fieberg, 2007; de Faria Oshima and de Oliveira Santos, 2016). In the present study, dolphins were categorised as 'resident' following the criteria provided by Gubbins (2002) and Chen et al. (2011), i.e. dolphins have the highest re-sighting rate ($>$ 20 observations) and they are seen at least once each year. The minimum number of locations for each individual was 21 and the maximum was 109. For dolphins seen more than once per day, only the first sighting of the day was included in the home range analysis (Gubbins, 2002; Rayment et al., 2009).

The gender of bottlenose dolphins was determined based on the overall photo–identification data (collected in this area since 1995), observation data and photographs/videos of their genital slits (Whitehead, 2008). Dolphins identified as 'females' were characterised by their gender-specific behaviour, such as nursing, which was associated with accompanying a calf for multiple years. Resident animals known as adults for a minimum of 12 years (excluding the period of pre-independence that on average lasts for 4 years) and were never seen in multi-annual association with a calf (average age of sexual maturity reported for females in the Adriatic Sea is 12 years; see Pribanić et al., 2000) are considered as 'probable males'. Other dolphins, which did not fulfil the criteria listed above, were considered to be of 'unknown' gender.

Locations of dolphin sightings were recorded using a Garmin 76 Cx handheld GPS (accuracy ± 5 m). Home ranges of 44 resident dolphins were obtained using non-parametric, utilisation distribution estimators: the 95% fixed kernel density estimator and 50% fixed–kernel density estimator (KDE) with smoothing parameters calculated using the reference bandwidth (Rayment et al., 2009; Worton, 1989). For each of the 44 resident dolphins, a 95% KDE was calculated as a measure of the individual home range size to exclude occasional sallies or areas the animal will never visit again. A 50% KDE was calculated to identify their core use areas (Gubbins, 2002). In addition, the 100% minimum convex polygon method (MCP) was also calculated. Although this provides a crude estimate of the home range, it is the most commonly used method to investigate possible interactions between individuals regardless of their spatial behaviour (Boitani and Fuller, 2000; Frère et al., 2010).

For the overall home range size (MCP, 95% KDE and 50% KDE), linear distances between sequential encounters of each resident dolphin and home range overlaps were calculated by combining the use of *adehabitatHR* package (Calenge, 2006) in programs R v. 3.0.2 (R Development Core Team 2006) for Mac OS X and Home Range Tool v. 2.0.20. in ArcView 10.2. All methods subtracted any landmasses included in the individual home range calculations (Gubbins, 2002; Chen et al., 2011).

2.1. Influencing factors

2.1.1. Association patterns, gender, and natal philopatry

In order to explore the relations between the home range and the association patterns, the half-weight index (HWI) was used to calculate Coefficients of Association (COAs) between the 44 resident dolphins in SOCPROG v. 2.4 (Whitehead, 2009).

Within the sample, individuals were categorized as "paired" and "unpaired" dolphins based on the results of the cluster analysis (Ward method; Milligan and Cooper, 1988) with paired dolphins generally having COAs ≥ 0.5 with their partner dolphin (mean COAs of paired dolphins ± SD = 0.75 ± 0.16; Chen et al., 2011).

Fission-fusion social grouping in bottlenose dolphins generally results in females having more fluid, open relationships (Smolker et al., 1992) whilst males form longer–term alliances (Connor et al., 2000). Hence the relationships between home ranges and COAs were analysed separately for females and males considering both home range size (MCP, 95% KDE and 50% KDE) and MCP home range overlap, the latter indicating the size (km^2) of the area calculated overlaying MCP home ranges of two associated individuals.

The strength of natal philopatry was assessed based on the overlap of the home ranges of the three former calves during their juvenile phase and adulthood. The maternal influence was assessed based on the home range overlap between the former calf's' home range in the adulthood period and its mothers' home range.

In addition, eventual differences between females' home range when with calves and in the interim calving period was assessed.

2.1.2. Anthropogenic pressure

Recent studies have found significant seasonal variations in the number of leisure boats frequenting the study area (Rako et al., 2013a). As a result, seasonal differences between summer season (June–-September) and winter season (October–May), were assessed for the home range of both males and females.

The effect of this fishing activity on the home range sizes of the 44 resident animals was assessed by confronting home range sizes calculated on two datasets: *Complete* (C) dataset that includes the overall data and *No Trawler* (NTw) dataset which excludes all encounters with dolphins recorded behind bottom trawlers.

2.2. Statistics

Statistical analysis was run through SPSS 17.0 for Windows (SPSS, Inc.). Differences in home range sizes (overall and seasonal) for females and males, within and between clusters, and between paired and unpaired dolphins were tested using non-parametric tests: Mann–Whitney U test and Kruskal–Wallis at $P < 0.05$. Differences in home range overlap of paired dolphins between the clusters were also tested using the Mann–Whitney U test as well as the seasonal differences in home range size and in mean linear distances between sequential encounters for both females and males. The relationship between the total number of dolphin encounters and home range sizes, as well as between home range (sizes and overlap) and COAs, was assessed applying a Spearman rank – order correlation. The influence of the trawling activities on the home range size was tested using Related Samples Wilcoxon Signed Rank Test.

3. Results

3.1. Ranging patterns

The encounters of the 44 resident dolphins were recorded between 2005 and 2014. Of these, 21 were females, 14 were 'probable males' (hereafter referred to as males) and 9 were of unknown gender. The number of encounters for an individual dolphin varied from a minimum of 21 to a maximum of 109 (Table 1). The mean home range size based on the MCP method of the 44 resident bottlenose dolphins was 405.9 km^2 (SD ± 114.97). The mean 95% KDE home range was estimated to be 1294.3 km^2 (± SD = 539.73) and the mean 50% KDE home range indicated the use of core areas of 240.9 km^2 (± SD = 109.81; Fig. 2; Table 1).

Overlapping individual home ranges of the 44 resident animals, calculated using 95% KDE and 50% KDE, resulted in two hub areas (Fig. 3), i.e. areas shared by all 44 individuals (Gubbins, 2002). The 95% KDE hub size was 375.43 km^2, 82% of which was included in the Cres and Lošinj SCI (HR3000161), covering 59% of its extension. The 50% KDE hub had a size of 17.50 km^2, and represented the very core area of the Cres and Lošinj SCI.

Results showed that male dolphins were encountered significantly more frequently (Table 1; Kruskal–Wallis test, $H = 5.25$, $P = 0.022$) and used significantly smaller areas in comparison to females (Table 1; Fig. 4, Mann–Whitney U test, MCP: $U = 85.0$, $P = 0.037$; 95% KDE: $U = 57.0$, $P = 0.002$; 50% KDE: $U = 57.0$, $P = 0.002$). Both females and males used larger areas during the summer months. Differences between summer and winter home ranges were found considering all three methods for estimating home range, with winter home range sizes being generally smaller than the summer home ranges (Fig. 4). However, this was only significant between summer and winter MCP ranges (Mann–Whitney U test; Females: $U = 106.9$, $P = 0.004$; males: $U = 28.0$, $P = 0.001$).

The total number of encounters of the individual dolphins did not differ significantly among seasons (Mann–Whitney U test: $U = 813{,}5$, $P = 0.056$). The individual seasonal ERs indicate significantly higher ER for individual dolphins during the winter months in comparison to

Table 1
Home range sizes (MCP, 95% KDE, 50% KDE) of 44 resident dolphins in Kvarnerić (North Adriatic Sea). Mean linear distance between consecutive encounters is indicated for each individual. Sex is female (F), male (M) and unknown (U).

Dolphin ID	Gender	N encounters	Mean linear distances (km)	MCP (km^2)	95% kernel (km^2)	50% kernel (km^2)
1	F	36	15,20	479,19	1609,16	300,06
2	F	35	12,76	359,46	1020,79	221,46
3	M	65	10,94	446,82	999,39	159,14
4	U	41	11,80	497,06	928,71	152,78
5	F	32	19,31	484,18	2530,21	482,31
6	F	58	7,17	327,18	784,90	149,64
7	U	27	10,27	489,94	1830,43	289,76
8	M	97	8,36	337,93	788,09	115,02
9	M	40	11,61	512,64	1521,51	252,33
10	M	107	16,53	250,32	536,89	97,00
11	M	57	10,39	266,78	584,10	131,02
12	M	65	12,83	364,02	914,17	169,82
13	F	46	9,36	493,61	1337,43	226,69
14	F	46	18,40	317,15	1244,33	311,43
15	M	36	13,30	405,68	1399,14	251,06
16	U	28	16,71	343,60	1567,54	293,61
17	F	50	13,58	662,17	1478,91	242,92
18	M	92	12,78	226,88	465,46	92,37
19	F	43	15,70	607,20	1740,24	268,21
20	F	34	10,45	654,71	2394,34	440,50
21	F	43	20,55	635,84	1968,70	317,08
22	U	28	14,30	247,76	988,50	219,77
23	F	54	13,29	455,21	1203,12	244,65
24	F	69	12,56	369,91	948,67	169,45
25	M	109	7,03	294,06	636,17	86,40
26	M	71	9,57	313,63	722,01	130,30
27	F	21	10,77	502,67	2099,22	382,33
28	F	58	22,77	276,84	752,93	131,56
29	U	24	22,93	276,84	752,93	131,56
30	F	27	19,61	309,84	2580,45	503,07
31	U	41	13,30	450,24	1312,03	220,08
32	M	54	11,01	322,34	812,60	158,94
33	M	38	12,78	475,72	1338,54	289,42
34	U	25	16,51	404,45	1843,58	397,11
35	F	26	15,26	309,84	1634,50	304,73
36	M	60	10,78	317,97	718,13	145,77
37	U	44	10,15	433,39	977,00	143,70
38	F	46	14,16	430,78	1362,52	261,21
39	F	30	13,54	352,26	1395,63	305,19
40	F	25	20,38	571,51	1977,84	489,81
41	M	25	15,74	360,06	1720,05	337,75
42	U	53	14,20	551,54	1517,54	265,12
43	F	31	11,96	347,22	912,29	143,09
44	F	30	11,41	323,24	1098,54	176,70
Total mean size ± SD				405.9 ± 114.9	1294.3 ± 539.7	539.7 ± 109.8

summer months (Kruskal–Wallis test, $H = 8.98$, $P = 0.003$) although the research effort was more intense during the summer (total distance covered in good research conditions was 26,006,5 km) than in the winter (total distance covered in good research conditions was 13,687,2 km; Table 2). The overall mean linear distances between sequential encounters were significantly smaller during winter (Mann–Whitney U test: $U = 733.0$, $P = 0.011$) than in summer (S: mean ± SD = 11.44 km ± 3.6 km; W: mean ± SD = 9.95 km ±

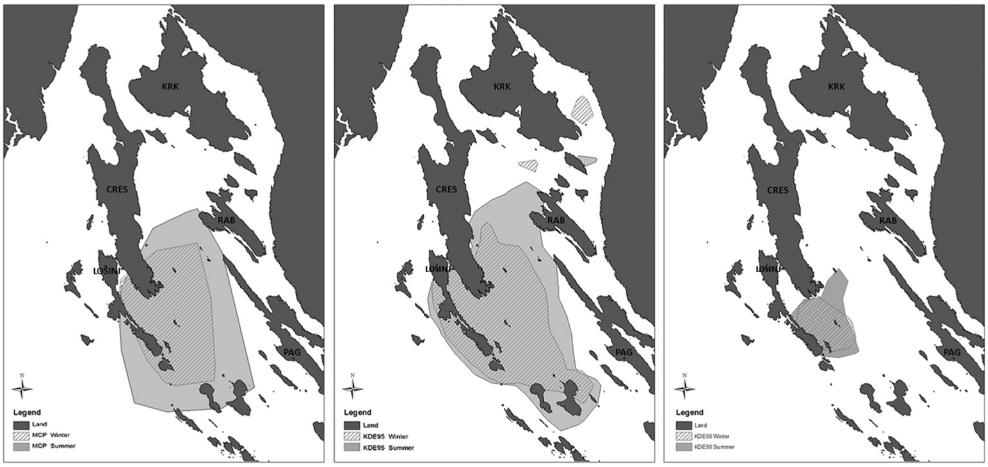

Fig. 2. The mean home range size of the 44 resident bottlenose dolphins calculated using MCP, 95% KDE and 50% KDE method, presented for summer and winter season separately.

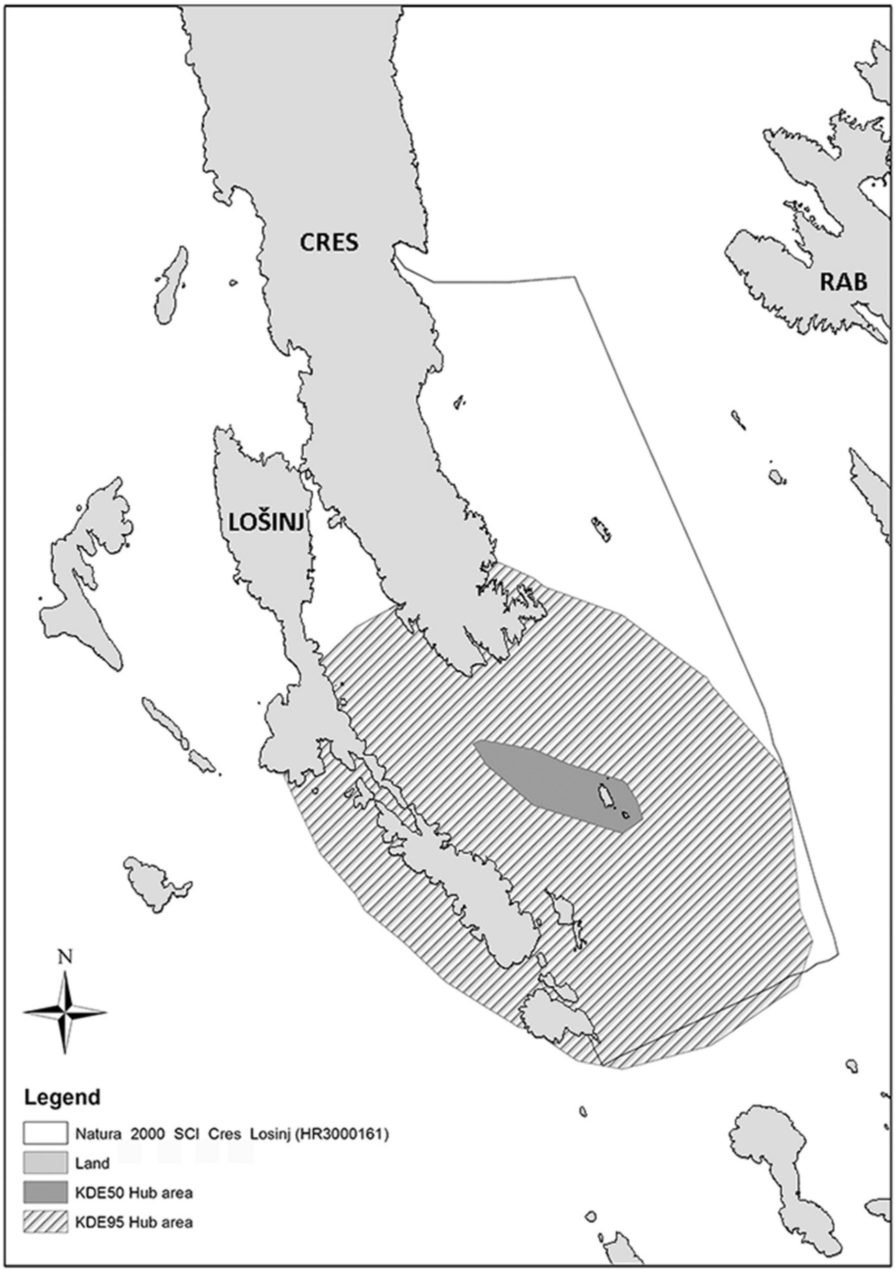

Fig. 3. Hub areas - areas shared by all 44 individuals, calculated using 95% KDE and 50% KDE.

3.4 km; Fig. 4).

During the study period, bottom trawlers were checked for the presence of dolphins on 422 occasions and individuals of the 44 resident dolphins were found on 100 occasions. The encounter rate of resident dolphins behind trawling boats (N sightings behind Tw/overall sightings) is shown in Fig. 5. Male dolphins were found to follow trawlers more frequently than females (Kruskal–Wallis test, $H = 10.547$, $P = 0.005$). Significant differences were found when

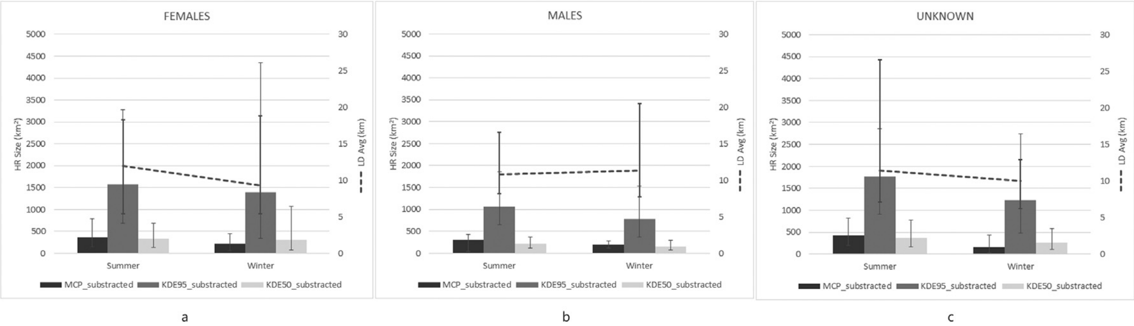

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Fig. 4. Comparison of home range sizes and mean linear distances between seasons and for different genders. The standard deviation is shown by vertical lines above the bars.

Table 2
Yearly and seasonal effort and ERs of individual dolphins.

	All	Summer	Winter			
Effort (km)	39,693.7	26,006.5	13,687.2			
Dolphin ID	N encounters	Encounters summer	Encounters winter	ER all	ER summer	ER winter
1	36	15	21	0.00091	0.00058	0.00153
2	35	22	13	0.00088	0.00085	0.00095
3	65	36	29	0.00164	0.00138	0.00212
4	41	32	9	0.00103	0.00123	0.00066
5	32	14	18	0.00081	0.00054	0.00132
6	58	46	12	0.00146	0.00177	0.00088
7	27	15	12	0.77143	0.00058	0.00088
8	97	53	44	0.00244	0.00204	0.00321
9	40	17	23	0.00101	0.00065	0.00168
10	107	49	58	0.00270	0.00188	0.00424
11	57	38	19	0.00144	0.00146	0.00139
12	65	30	35	0.00164	0.00115	0.00256
13	46	22	24	0.00116	0.00085	0.00175
14	46	25	21	0.00116	0.00096	0.00153
15	36	7	29	0.00091	0.00027	0.00212
16	28	10	18	0.00071	0.00038	0.00132
17	50	35	15	0.00126	0.00135	0.00110
18	92	36	56	0.00232	0.00138	0.00409
19	43	35	8	0.00108	0.00135	0.00058
20	34	21	13	0.00086	0.00081	0.00095
21	43	22	21	0.00108	0.00085	0.00153
22	28	21	7	0.00071	0.00081	0.00051
23	54	28	26	0.00136	0.00108	0.00190
24	69	38	31	0.00174	0.00146	0.00226
25	109	56	53	0.00275	0.00215	0.00387
26	71	48	23	0.00179	0.00185	0.00168
27	21	14	7	0.00053	0.00054	0.00051
28	58	23	35	0.00146	0.00088	0.00256
29	24	13	11	0.00060	0.00050	0.00080
30	27	17	10	0.00068	0.00065	0.00073
31	41	13	28	0.00103	0.00050	0.00205
32	54	25	29	0.00136	0.00096	0.00212
33	38	16	22	0.00096	0.00062	0.00161
34	25	20	5	0.00063	0.00077	0.00037
35	26	11	15	0.00066	0.00042	0.00110
36	60	43	17	0.00151	0.00165	0.00124
37	44	37	7	0.00111	0.00142	0.00051
38	46	30	16	0.00116	0.00115	0.00117
39	30	12	18	0.00076	0.00046	0.00132
40	25	10	15	0.00063	0.00038	0.00110
41	25	19	6	0.00063	0.00073	0.00044
42	53	32	21	0.00134	0.00123	0.00153
43	31	13	18	0.00078	0.00050	0.00132
44	30	21	9	0.00076	0.00081	0.00066

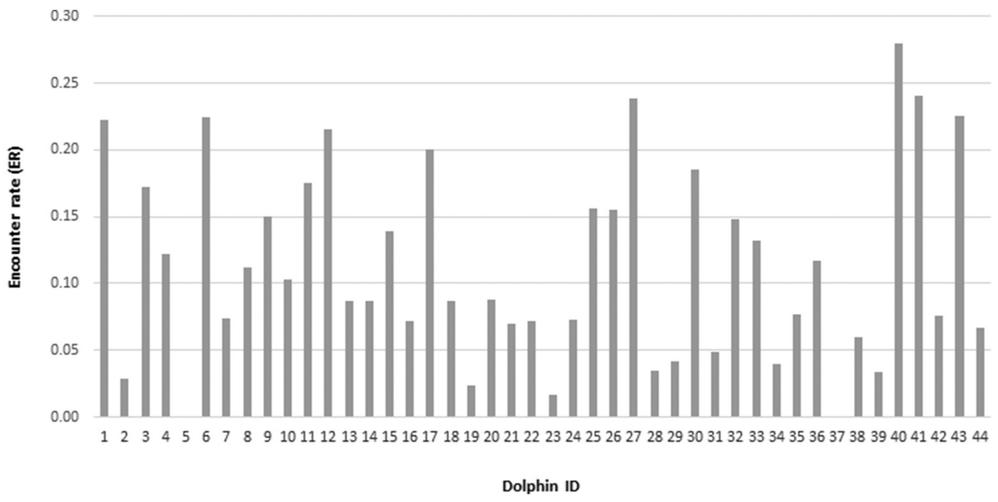

Fig. 5. Dolphin encounter rate behind bottom trawlers (ER represents ratio between dolphin sightings behind bottom trawlers and the overall sightings).

Table 3
Differences in home range sizes (MCP, 95% KDE, 50% KDE) of two datasets: C dataset (C) - that includes the overall data and *No Trawler* (NTw) dataset – that excludes all encounters with dolphins recorded behind bottom trawlers. Home range sizes are presented for different genders, for summer and winter season.

Gender		KDE95 C dataset	KDE95 summer C dataset	KDE95 winter C dataset	KDE95 NTw dataset	KDE95 summer NTw dataset	KDE95 winter NTw dataset
Female	Mean	1510.10	1563.51	1386.65	1409.37	1391.55	1337.69
	Min	752.93	679.00	339.98	735.47	499.34	462.53
	Max	2580.45	3276.95	4343.02	2292.42	2605.53	4343.02
Male	Mean	939.73	1066.30	779.34	901.07	1010.53	710.42
	Min	465.46	650.37	372.22	417.95	611.99	346.35
	Max	1720.05	1854.14	1532.17	1743.34	1872.69	1572.90
Unknown	Mean	1528.00	1769.01	1231.12	1501.83	1802.92	1185.25
	Min	928.71	908.98	480.84	869.15	914.67	496.80
	Max	2786.71	2859.17	2734.57	2759.45	2962.72	2865.63
Gender		MCP C dataset	MCP Summer C dataset	MCP Winter C dataset	MCP NTw dataset	MCP Summer NTw dataset	MCP Winter NTw dataset
Female	Mean	457.93	357.03	218.95	390.72	279.28	195.24
	Min	276.84	151.36	59.69	158.90	60.77	22.78
	Max	662.17	791.23	441.32	662.17	673.81	441.32
Male	Mean	349.63	299.91	195.38	331.97	260.98	182.57
	Min	226.88	42.03	110.38	195.72	42.03	76.77
	Max	512.64	432.75	278.67	485.18	416.59	270.29
Unknown	Mean	454.22	421.89	165.07	428.42	408.86	153.96
	Min	247.76	190.93	28.19	198.80	190.93	28.19
	Max	670.01	829.01	431.41	615.78	829.01	431.41
Gender		KDE50 C dataset	KDE50 Summer C dataset	KDE50 Winter C dataset	KDE50 NTw dataset	KDE50 Winter NTw dataset	KDE50 Summer NTw dataset
Female	Mean	282.89	328.51	296.98	261.53	195.24	292.97
	Min	131.56	131.18	67.75	121.13	22.78	77.23
	Max	503.07	686.43	1077.16	427.02	441.32	605.72
Male	Mean	172.59	214.20	153.24	160.32	182.57	202.37
	Min	86.40	113.32	73.95	79.26	76.77	92.11
	Max	337.75	373.39	297.42	334.36	270.29	415.63
Unknown	Mean	286.95	374.43	264.29	276.31	153.96	376.99
	Min	143.70	163.38	108.45	138.33	28.19	149.07
	Max	600.65	778.22	589.61	550.10	431.41	759.21

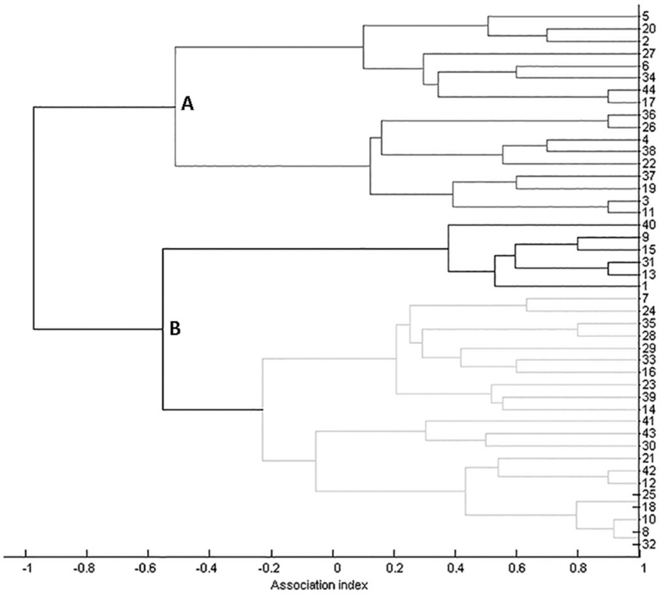

Fig. 6. Cluster analysis based on half – weight coefficients of associations (COAs) for 44 resident dolphins.

comparing home ranges calculated using the complete dataset (C dataset) to home ranges calculated using *No Trawler* dataset (NTw-dataset). These differences in home range sizes were found when using all three methods for estimating home range and indicate significantly larger home range size for the C dataset (Table 3; Related Samples Wilcoxon Signed Rank Test; MCP: $P \leq 0.001$; KDE95: $P = 0.012$; KDE50: $P \leq 0.001$). When comparing two data sets (C vs. NTw), considering males and females separately, significant differences in home range sizes were found in both genders. In females, these differences were found when comparing two datasets (C vs. NTw: Related Samples Wilcoxon Signed Rank Test; MCP: $P = 0.001$; 95% KDE: $P = 0.014$; 50% KDE: $P = 0.003$) and particularly between the home range sizes calculated between the summer datasets (C vs. NTw: Related Samples Wilcoxon Signed Rank Test; MCP: $P = 0.006$; 95% KDE: $P = 0.004$; 50% KDE: $P = 0.001$). In males, significant differences in home range size was found using the MCP and 50% KDE method (Related Samples Wilcoxon Signed Rank Test; MCP: $P = 0.01$; 50% KDE: $P \leq 0.001$) also during the summer season (Related Samples Wilcoxon Signed Rank Test; MCP $P = 0.002$; 50% KDE: $P = 0.007$).

Moreover, a negative correlation was found between home range size and overall number of dolphin encounters, in particular for males, indicating that more frequently encountered males had smaller home ranges (for all three methods Spearman rank order correlation: MCP: $R = -0.622$, $P = 0.018$; 95% KDE: $R = -0.763$, $P = 0.002$; 50% KDE: $R = -0.899$, $P < 0.001$). In females, negative correlation was less strong and was found only between the overall number of encounters and home range sizes calculated using KDE methods (Spearman rank order correlation: 95% KDE: $R = -0.583$, $P = 0.006$; 50% KDE: $R = -0.579$, $P = 0.006$).

Females were found to use larger home ranges in nursing periods in comparison to interim periods between calving, although the variation was not significant.

3.2. *Ranging patterns of associated individuals*

A cluster analysis, based on coefficients of associations (COAs) between the 44 resident individuals, indicated the existence of two distinct social clusters (Fig. 6). Cluster A included 17 resident individuals (7 pairs) and cluster B included 27 resident individuals (10 pairs). No significant differences were found in MCP, 95% KDE and 50% KDE home ranges between the two clusters or among individuals of the same cluster. Mean linear distances for the individuals in cluster B were

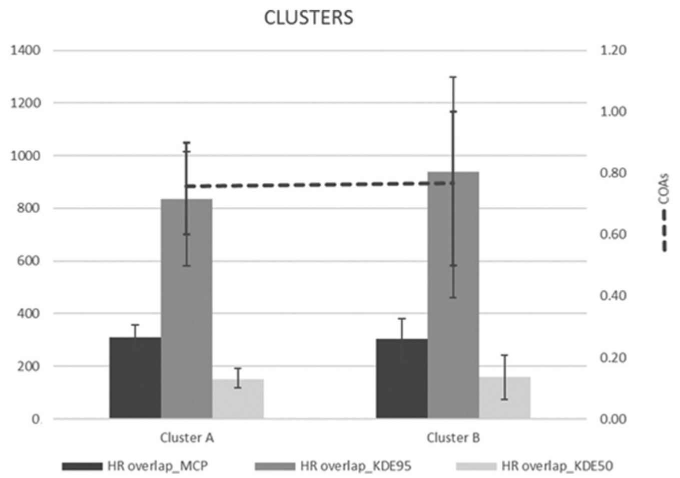

Fig. 7. Comparison of home range overlap (MCP, 95% KDE and 50% KDE) and coefficient of associations (COAs) between two clusters (A and B). The standard deviation is shown by vertical lines above the bars.

14.5 km between two sequential encounters and 12.3 km in cluster A. When overlaying home ranges between paired dolphins (COAs > 0.5), no significant differences were found in the sizes of the overlap area between the two clusters (Fig. 7).

As dolphins have multiple partners during their lifetime, besides their preferred associations (pairs), the COAs were also calculated among all the 44 resident dolphins. In general, females were found to form more fluid social groups, group composition was regularly changing, and had significantly smaller COAs in comparison to males (Mann–Whitney *U* test, $U = 8794.0$; $P = 0.022$). Home range overlap between the individuals for all the 924 associations was calculated using the MCP method (Frère et al., 2010). A significantly positive correlation was found between COAs and MCP home range overlap among females (Fig. 8; Spearman rank ordered correlation: $R = 0.149$, $P = 0.023$).

The correlation between COAs and MCP home range overlap in males was not significant (Spearman rank order correlation: $R = 0.065$, $P = 0.543$).

Along with generally small size of MCP home range overlap, male pairs with the highest COAs (> 0.9) also had the highest numbers of encounters (Fig. 8).

Maternal influence was analysed based only on those mother-calf pairs identified among the 44 resident dolphins where the former calves also remained resident in the area after they became independent (separated from their mothers), hence only three such pairs were used. Two of the three former calves were females; the third was of unknown gender. Two former calves (one female and one of unknown gender) used 100% of their natal range after they became independent, and showed considerable home range overlap with their mothers' home ranges (Table 4). The third former calf (female) indicated a lower overlap (87% MCP, 71% KDE95, 20% KDE50) between its natal home range and the home range after independence and has over 54% home range overlap to its mothers' home range (MCP, KDE95 and KDE50; Table 4).

Table 4
Maternal influence on the former calves home range patterns.

ID	MCP (km^2)	KDE95 (km^2)	KDE50 (km^2)
Calf 1 HR size	85.57	392.89	65.12
HR size in the adult phase	317.15	1244.33	311.43
Mother's HR size	493.61	1337.43	226.69
Natal HR overlap[a] (%/km^2)	99.9% (85.49)	100% (392.89)	99.8% (65.001)
Mother's HR overlap[b] (%/km^2)	64% (296.9)	84% (1125.88	84% (191.75)
Calf 2 HR size	141.74	699.83	124.85
HR size in the adult phase	670	2786.71	600.64
Mother's HR size	276.84	752.93	131.56
Natal HR overlap[a] (%/km^2)	88% (125.73)	100% (699.83)	98.5% (123.09)
Mother's HR overlap[b] (%/km^2)	81% (226.49)	100% (752.92)	100% (131.56)
Calf 3 HR size	58.75	914.17	200.55
HR size in the adult phase	369.9	948.67	169.45
Mother's HR size	455.21	1203.12	244.65
Natal HR overlap[a] (%/km^2)	87% (51.67)	71% (652.3)	20% (40.52)
Mother's HR overlap[b] (%/km^2)	96% (355.19)	65% (784.66)	54% (134.33)

[a] 'Natal HR overlap' – percentage of natal home range (home range used as a calf) included in the home range in the adult phase.

[b] 'Mother's HR overlap' – percentage of home range used in the adult phase and the mother's home range.

4. Discussion

This study assesses the home range patterns of resident bottlenose dolphins inhabiting the Cres-Lošinj archipelago, a recently declared Cres and Lošinj SCI (HR3000161), important as a feeding and nursing ground (Mackelworth et al., 2013). As is consistent with other studies, the overall results indicate variations in the home range estimates related to the different methods used (Chen et al., 2011; Gubbins, 2002; Rayment et al., 2009). Although in recent times other methods have been developed for this purpose, the MCP and the KDE remain the most commonly used methods available, making them suitable for comparison (Flores and Bazzalo, 2004; Gubbins, 2002; Powell, 2000).

Variations in home range patterns among the individual resident dolphins of this study are primarily related to differences in gender and are reflected in the way in which different genders respond to the dominant external stressors within their habitat i.e. fishery and nautical tourism (Mackelworth et al., 2003; Fortuna, 2006). Nautical tourism, and more precisely personal recreational boating, has already been found to have adverse effects on dolphin communication and habitat use in this Cres and Lošinj SCI (Fortuna, 2006; Rako et al., 2013a; Rako-Gospić and Picciulin, 2016). According to Frid and Dill (2002), fast moving objects are likely to be perceived as predators and reactions to their presence can include avoidance and displacement of animals

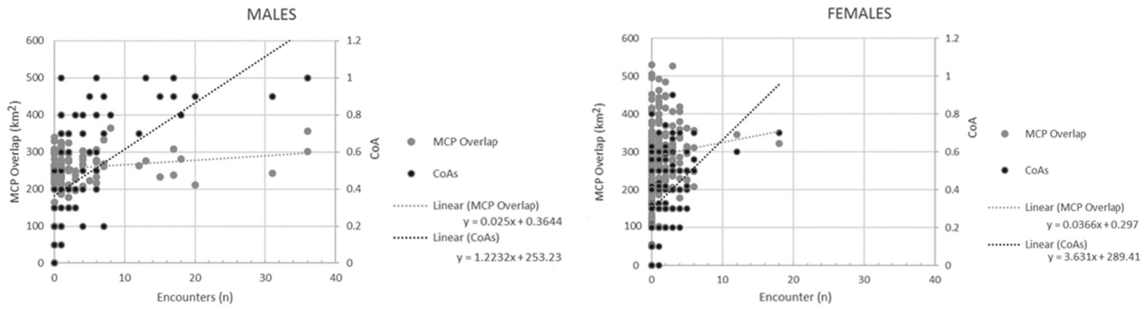

Fig. 8. Correlation between coefficient of associations (COAs), home range overlap and *N* encounters in males and females.

(Arcangeli et al., 2009; Bejder et al., 2006; Fortuna, 2006; Papale et al., 2011; Stensland and Berggren, 2007).

The results of this study confirm the seasonal influence of nautical tourism on both female and male resident dolphins through changes in their home range sizes. These changes overlap with the period of most intense recreational boating. All 44 dolphins were found to use larger areas and to have significantly increased mean linear distances between sequential encounters during the summer. The increase in the size of the home range is consistent with the results on the individual ERs that are found to be higher during the winter months in comparison to summer months despite the more intense research effort during the summer. This result is in accordance with changes in dolphin distribution found by Rako et al. (2013a) who reported a significant drop in dolphin encounters during the summer season in the areas characterised by intense boating despite the increased research effort. Concurrently, Rako et al. (2013a) also showed that there was an increase in dolphin encounters in the less busy, peripheral part of the study area in the summer season.

Bottom trawlers were also found to have a significant effect on the home range size of resident dolphins. Male dolphins were found to depredate on trawling nets and forage behind bottom trawlers more frequently than females. It is likely that reduced depredation of trawling nets in females is related to the elevated risk of entanglement of young and less experienced offspring that usually accompany them when foraging (Fertl and Leatherwood, 1997; Nelson, 1990). However, the influence of bottom trawlers was found to be particularly significant for both genders during the summer season. This is likely to be related to the influence of increased recreational boating. The use of this higher risk feeding strategy may be a pragmatic decision to supplement the energy consumed in attempts to avoid anthropogenic disturbance within their preferred habitat. This is particularly significant for female dolphins that tend to apply this higher risk feeding strategy less frequently than males. Increased anthropogenic pressure is likely to be a driver to use this strategy to support the high energetic requirements related to the care of their offspring.

The overall results of this study show that females use significantly wider areas, especially during the nursing periods. This segregation by gender may be due to habitat features and differences in energetic requirements and feeding strategies between males and females (Cockcroft and Ross, 1990). For example, females in Sarasota Bay, USA, were found to stay in highly productive seagrass meadows and thus have much smaller home ranges (Scott et al., 1990). Similar findings were reported by Wells et al. (1987) and Bearzi et al. (2010). Conversely, home range sizes between genders were not found to be significantly different in a previous study made in the Central Adriatic Sea (Holcer, 2012). Yet, the use of large home ranges in female bottlenose dolphins is consistent with the findings of Gaspari et al. (2015) that identify females as the principal gene flow mediators in the Adriatic Sea.

Resident male dolphins were found to have a relatively high frequency of occurrence in significantly smaller areas. Those male pairs having the highest COAs between them (> 0.9) also had the highest number of encounters and the smallest home range sizes. This result may indicate that male movement patterns in Cres-Lošinj waters are affected by the creation of strong and highly territorial alliances, such as those found also in other mammals (Amsler, 2010; Wallace, 2008). Conversely, in the Central Adriatic Sea study associations between females tend to be stronger (Holcer, 2012).

According to Clutton-Brock (1989)and Frère et al. (2010), the size of the MCP home range overlap area between individual dolphins may indirectly predict the probability of their social interactions. However, MCP home range provides information on all the possible spatial use by an individual without considering the possible interaction, or absence of interaction, between individuals in the same space (Fieberg and Kochanny, 2005). Thus, the calculation of the size of the MCP home range overlap, when predicting social interactions between individuals, should always be considered with some caution. For this reason, when predicting the probability of social interactions between the individuals through analysis of the overlap of their MCP home ranges, quantifying the proportion of each animals' home range would be more informative (Fieberg and Kochanny, 2005). For example, in this study the size of the MCP home range overlap area was predictable of social bonds only in females. The association patterns in territorial males, that form strong alliances between them, were not always predictable by the size of their home range overlap. Although the COAs (> 0.9) of territorial males were very high, the size of their individual home ranges and hence the MCP home range overlap area were found to be rather small. In some cases, a much larger home range overlap could be found between two less territorial males that have wider individual home ranges although the probability of finding them together in the same space is quite small.

The 44 resident individuals considered in this study also included three resident females and their offspring. Their overall home range size was calculated in order to assess the maternal influence on the immature animals (offspring) ranging patterns after they become independent. In dolphins, the mother–calf bond generally extends beyond the nursing period. Home ranges of former calves are often positively related to the size of home range of their mother indicating their natal philopatry as they retain a large amount of their natal ranges (Connor et al., 2000; McHugh et al., 2011; Sargeant and Mann, 2009; Tsai and Mann, 2013). In this study, all of the ex-calves use a considerable amount of their natal home ranges after becoming independent overlapping considerably with the home range of their mother. More detailed research, to consider interrelatedness over the multiple concurrent generations is needed to assess the degree of philopatry to natal areas after the calves become independent. This could provide more understanding of the behaviour of inshore bottlenose dolphin populations and therefore contribute to their conservation.

5. Conclusions

Knowledge of the ranging patterns and factors affecting habitat preferences of conservation target species is of fundamental importance not only to understand ecological processes but also to consider appropriate management and conservation measures. The 95% and 50% KDE home range estimates of resident animals overlapped to create two hub areas (one hub for each method) that, combined with the results from the cluster analysis, indicate that the resident dolphins consist of two social units with similar ranging patterns. The results indicate that both hub ranges fall within the Cres and Lošinj SCI (HR3000161), confirming that this is a representative home range area for these resident bottlenose dolphins. As such, appropriate conservation measures applied within this area, as a part of Natura 2000 regime, should have a positive influence on this local bottlenose dolphin population minimizing the containment of their habitat use and contributing to the preservation of this important marine area. However, due to the strong interaction between dolphins and anthropogenic use of this area, the development of the appropriate conservation regime needs to involve the human dimension. Socio-economic studies should focus on the primary sectors utilising this area, fishery and tourism, in order to share knowledge and opinions regarding the use of the area. Only the exchange of knowledge and open stakeholder dialogue will lead to the development of the appropriate regulations to balance conservation with sustainable use of this Cres and Lošinj SCI.

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ARTICLE

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Bottlenose dolphins (*Tursiops truncatus*) in North Dalmatia, Croatia: Occurrence and demographic parameters

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Abstract

The common bottlenose dolphin (*Tursiops truncatus*) population along the eastern Adriatic coast is believed to comprise discrete communities, yet many of them are unstudied. This study provides the first description of occurrence and demographic parameters for the community inhabiting waters of North Dalmatia. Dedicated boat-based surveys conducted in summer months from 2013 to 2017 resulted in 13,896 km of research effort and 284 dolphin sightings from which 336 individuals were identified. Site-fidelity analysis revealed that 52.1% of encountered marked adults occur in the area regularly or occasionally. No significant difference among years could be found for mean group sizes (5.73–7.46) and group encounter rates (1.159–1.942 groups/100 km). Pollock's Robust Design models estimated annually variable adult apparent survival (0.737–0.986) and constant temporary emigration rate of 0.172. The estimated abundance varied annually from 116 to 138 individuals and showed a negative slope, but a significant trend could not be confirmed. Age-dependent models estimated first-year calf survival at 0.875. These results provide a baseline for informed management of two Sites of Community Importance, and a benchmark for future monitoring in North Dalmatian waters, an area under significant anthropogenic pressure.

KEYWORDS

abundance, Adriatic Sea, bottlenose dolphin, demography, encounter rate, mark-recapture, photo-identification, Pollock's Robust Design, residency, survival, *Tursiops truncatus*

1 | INTRODUCTION

The common bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), hereafter bottlenose dolphin, is among the most extensively studied cetacean species due to its presence in accessible coastal areas (Reeves, Stewart, Clapham, & Powell, 2002). Owing to overlap with areas under significant anthropogenic pressure, the coastal populations of bottlenose dolphins are at particular risk (Pleslić et al., 2015; Wilson, Thompson, & Hammond, 1997). The IUCN Red List of Threatened Species categorizes the Mediterranean bottlenose dolphin subpopulation as “Vulnerable,” and current population trend as decreasing (Bearzi, Fortuna, & Reeves, 2012). Despite an increasing number of studies aimed at coastal populations, many areas within the Mediterranean basin remain data deficient, complicating assessment of their conservation status.

Demographic parameters provide cornerstone information needed to assess conservation status and define management strategies for protection of a species (Brown, Bejder, Pollock, & Allen, 2016; Lusseau et al., 2006). As they may vary between populations or communities (Symons, Sprogis, & Bejder, 2018), it is crucial to obtain robust estimates separately for each assessment unit. Demographic parameters can fluctuate naturally due to stochastic events, which is not problematic if the population is large enough to absorb such fluctuations (Lacy, 1993). However, small populations are sensitive to fluctuations and any negative change can significantly increase risk of extinction (Goodman, 1987). This underlines the importance of determining assessment units and obtaining precise estimates of abundance, emigration, fecundity, and age-dependent survival rates to enable monitoring temporal trends and modeling population viability of small populations in relation to the changing environment.

Capture-recapture methods are routinely used in cetacean studies to estimate population demographic parameters (Santostasi, Bonizzoni, Bearzi, Eddy, & Gimenez, 2016; Tezanos-Pinto et al., 2013; Vermeulen & Bräger, 2015). The choice of appropriate model applied to capture-recapture data depends on the duration of the study and assumptions about the demography and movement patterns of the studied population (Santostasi et al., 2016). Closed population models assume that no births, deaths, emigration, or immigration occur in the population during the study period. Open models relax the assumptions of closed models by allowing the studied population to change between the sampling periods, but are unable to separate emigration from mortality. Pollock's Robust Design (RD) comes closer to biological reality by combining closed and open models and provides generally more accurate and precise estimates (Kendall & Nichols, 1995; Kendall, Pollock, & Brownie, 1995; Pollock, 1982). It estimates apparent survival and temporary emigration rates between primary periods which are far enough apart in time to allow the population to change. Capture probabilities and abundance are estimated based on secondary periods within each primary period that is short enough to satisfy the assumption of demographic closure.

Bottlenose dolphins show a high diversity in site fidelity across their distribution, ranging from year-round presence in a defined area, as in Gulf of Ambracia, Greece (Gonzalvo et al., 2016), Moray Firth, Scotland (Wilson et al., 1997), and Sarasota Bay, Florida (Wells & Scott, 1990) to seasonal (Lodi, Cantor, Daura-Jorge, & Monteiro-Neto, 2014) or occasional presence (Papale et al., 2017). The site fidelity can depend on habitat type, prey availability, social structure, and natal philopatry, and is therefore indicative of the ecology of a local population (Dinis et al., 2016; Rako-Gospić et al., 2017). It can thus help assess the importance of a habitat and help tailor management plans to local populations which may have different conservation needs depending, among other factors, on site fidelity.

In Croatia, bottlenose dolphins are protected under the Croatian Nature Conservation Law and several international agreements (Holcer, 2012). Furthermore, the European Union Habitats Directive (Council Directive 92/43/EEC; Council of the European Communities) lists bottlenose dolphins in Annex II, which requires the establishment of Special Areas of Conservation (SAC). At the moment, six Sites of Community Importance (SCI) are designated for protection of local bottlenose dolphin communities in the Croatian Adriatic Sea, a step preceding the declaration of SACs under the Natura 2000 scheme (Council Directive 92/43/EEC; Council of the European Communities).

Four out of the six SCIs were designated based on gray literature.[1] Data on demographic parameters of local communities are available only for the remaining two SCIs, with local communities defined pragmatically, rather than biologically, as assemblages of individuals occupying study areas for the duration of a study (Hammond, 2010;

Krebs, 1972). A resident local community inhabiting the Cres-Lošinj SCI (HR3000161) went through a 39% decline, from 168 (95% CI = 132–229) individuals in 1995 to 102 (95% CI = 86–127) individuals in 2003 (Fortuna, 2007). A later study showed a recovery of this community from 2004 to 2011, with estimates varying from 112 to 310 individuals (Pleslić et al., 2015) and the variations in abundance proposed to reflect shifts in habitat use rather than actual changes in abundance. Approximately 200 km south, in the area encompassing the Vis SCI (HR3000469), Holcer (2012) estimated the abundance of the local community at around 400 individuals.

A recent study by Pleslić et al. (2019) found another distinct bottlenose dolphin community of at least 49 adult individuals in North Dalmatian waters. Based on estimated home ranges and social structure, this community is spatially and socially distinct from those in the Cres-Lošinj and Vis areas. Furthermore, analysis of movement of individuals between those areas revealed a limited exchange. Nevertheless, the number of transient individuals was notable, indicating that the North Dalmatian community is not completely isolated.

Several anthropogenic pressures known to adversely affect bottlenose dolphins are present in North Dalmatia. The infrastructure supporting marine tourism is well developed with 13 marinas, 8 marine gas stations, and more than 8,000 berths (Kovačić, 2012). As a result, recreational boating is intense in the summer, which can lead to physical harassment and acoustic disturbance due to high levels of underwater noise, both factors known to cause displacement of bottlenose dolphins (Bejder et al., 2006; Rako et al., 2013a). This is coupled with depleted fish stocks (Dulčić, Soldo, & Jardas, 2005) and negative interactions with fisheries (entanglements in fishing gear and indications of intentional injuring; Blue World Institute data). These factors will present challenges for the management of the two SCIs (HR4000001 and HR3000419; Figure 1) within the waters of North Dalmatia once they are declared SACs.

Here, we present the first description of the occurrence, site fidelity and demographic parameters for a local community inhabiting the waters of North Dalmatia. The results of this study contribute to filling the gaps in understanding of the complex mosaic of local bottlenose dolphin communities along the eastern Adriatic coast, and provide baseline information needed for informed management of the two SACs within the area.

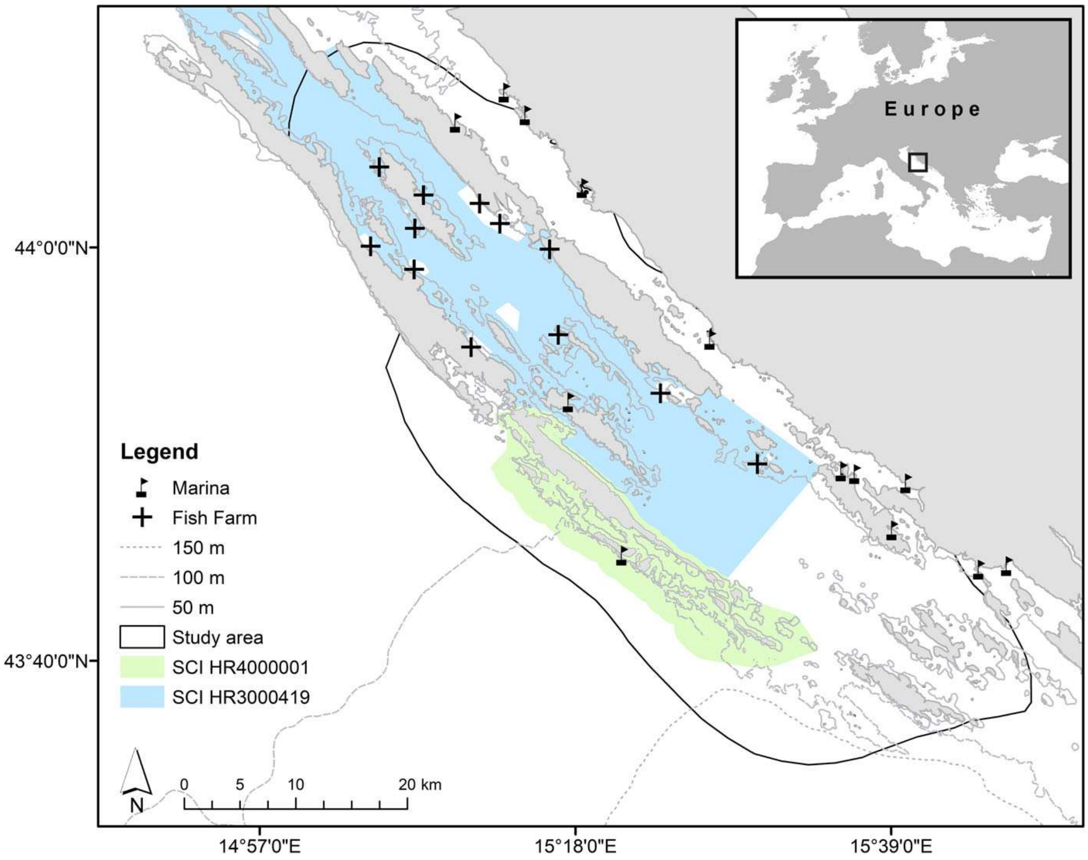

FIGURE 1 The region of North Dalmatia with study area marked with black line, 50 m, 100 m, and 150 m isobaths, locations of fish farms (black crosses), marinas (buoys), and two Sites of Community Importance (SCI).

2 | MATERIALS AND METHODS

2.1 | Study area

The home range of the local community in north Dalmatia (see Pleslić et al., 2019) was used as the boundaries of the study area, except for a part west of the island of Dugi Otok where research effort was significantly lower (Figure 1). The study area encompasses approximately 2,500 km^2 of the North Dalmatian archipelago, from the island of Sestrunj in the north to the island of Žirje in the south (Figure 1). The water depths are 60 m on average, exceeding 100 m only in the southern part, beyond the outer stretch of islands. Average sea-surface temperature in summer is 24°C (Penzar, Penzar, & Orlić, 2001). The seabed is diverse, with muddy and sandy substrates in deeper areas, sea grass (*Posidonia oceanica*) meadows in 5–30 m depths and numerous rocky ridges and shallows. There are 12 fish farms within the study area (Figure 1).

2.2 | Field procedures

Data were collected during boat-based surveys, in May to September from 2013 to 2017, using a 5.2 m rigid-hull inflatable powered by a 60 HP outboard engine. Survey tracks were chosen ad libitum, depending on the current weather conditions, while trying to survey all parts of the study area at least once each month. Survey tracks were noted as "on effort" when at least two researchers were actively looking for dolphins in a standing position, sea state was ≤3 on the Beaufort scale, visibility was not obscured by fog or rain, and a speed of 12–15 knots was maintained. Fish farms were inspected for presence of dolphins by driving parallel to clusters of cages at a reduced speed (approximately 8 knots). Operating trawlers were checked for presence of dolphins by stopping approximately 150 m behind the trawler for 5 min, as dolphins are known to perform long dives when feeding behind the bottom trawlers (Fortuna, Bearzi, & Delfino, 1996). Locations and times during navigation were logged using a Garmin 76Cx GPS device from 2013 to 2016, and a Samsung Tab 10.2 with NaviLog data logging app in 2017.

Upon spotting dolphins, the vessel approached the group, time and location were noted, and the photo-identification procedure started following methodology described by Würsig and Jefferson (1990). A sighting was defined as all Individuals in close proximity (usually <100 m), engaged in the same activity or maintaining the same travel direction (Pleslić et al., 2015). Group size and age classes were estimated in situ and later compared with results of photo-identification to verify reliability of estimates. Effort was made to photograph all present individuals, when possible from both sides. Digital SLR cameras, Canon EOS 30D and Canon EOS 6D equipped with a Canon EF 70–200 mm f/2.8 IS II USM lens were used to take photographs. The photo-identification procedure was terminated when all individuals were believed to have been successfully photographed or when the weather conditions deteriorated. Sightings resulting from "on effort" survey tracks were classed as "effort sightings." Those recorded within 200 m of fish farms were classed as "FF sightings," as their location was assumed to be influenced by the fish farm. Sightings recorded behind an operating trawler were classed as "TW sightings" and all others were classed as "off effort sightings."

2.3 | Photo-identification

The grading of photographic quality and distinctiveness of individuals was done following the recommendations of Urian et al. (2015). The photographs were assigned one of three quality grades. Those that met any of the following criteria were graded as Q3: fin out of focus, not perpendicular to camera, covered with water or spray, or too distant. Those with complete dorsal fin visible, in focus, perpendicular to camera and reasonably close were graded Q2, and those were the fin was additionally close to camera and well-lit were graded Q1. The individuals were assigned one of three levels of distinctiveness (D) based on presence and size of permanent natural marks (notches, cuts, and deformities) on dorsal fins.

Those without natural marks or natural marks too small to be discernible from Q2 photographs were classed as D3. Those with a few natural marks but large enough to be discernible from Q2 photographs were classed as D2, and those with many and/or large natural marks were classed as D1. To reduce the chance of misidentification, the threshold for quality grades was set to Q2 and all Q3 photographs were discarded from all subsequent analyses.

Individuals were matched with an existing reference dorsal fin catalog and assigned an age class. If encountered for the first time, they were assigned a name and added to the catalog. Individuals with approximately one third body length of an adult, dark gray coloration, visible fetal stripes, and surfacing at presumed mother's flank were classed as newborns (N), those with approximately one half to three quarters body length of an adult, light gray coloration, and repeatedly observed in groups with presumed mother were classed as calves (C), all others, including sub-adults, were classed as adults (A). Individuals for which a photograph of the genital area was available were classed as females (F) or males (M). Additionally, those observed repeatedly with a newborn or a calf were classed as females. All other individuals were classed as unknown sex (U).

2.4 | Group encounter rates

The study area was overlaid with a 2 × 2 km grid. For each cell and each year, total distance traveled "on effort" (L) and total number of "effort sightings" (n) were calculated. Cells where L was lower than the cell diagonal (2.82 km) were excluded from the analysis to reduce variability arising from cells with a low amount of research effort. For each cell, group encounter rates (GER) were calculated as GER = n/L. From these, annual and overall GERs were averaged. Moran's I index was computed from the obtained GERs to determine if the cells were autocorrelated.

2.5 | Site fidelity

To explore site fidelity, annual sighting rates were calculated as number of years when an adult individual was encountered divided by the number of years (n = 5) surveyed (Parra, Corkeron, & Marsh, 2006). Individuals were then assigned three arbitrary categories, reflecting statistical criteria, rather than biological. Those encountered in ≥3 years were classed as "regular," those seen in 2 years as "occasional," and those seen in 1 year as "rare."

2.6 | Modeling survival, emigration and abundance

As found by Pleslić et al. (2019), the bottlenose dolphin community in North Dalmatia is in limited contact with neighboring communities along shore but has a notable influx of transients from the offshore part of the Adriatic Sea. Therefore, to account for these movements, natality and mortality, Pollock's Robust Design (Pollock, 1982) was used to estimate abundance for each summer season, and apparent survival and temporary emigration rates between consecutive summer seasons. Only data from "effort sightings" and D1 and D2 individuals, collectively referred to as "marked," were used for these analyses.

2.7 | Model assumptions

Pollock's Robust Design relies on several assumptions:

(1) Individuals are always correctly identified. Only "marked" individuals identified from Q1 and Q2 photographs were used, thus misidentifications can be considered negligible.

(2) Capture occasions are instantaneous relative to the duration of study. Here, the capturing occasions were defined as shortest possible time frames enough to cover the study area once, resulting in the median capture occasion duration of 14.5 days (Table S1), which can be considered instantaneous relative to study duration.

(3) All individuals have the same and independent probability of being captured within one capture occasion. Due to study design, a uniform coverage of the study area in each capture occasion to allow all individuals to have equal capture probability could not be achieved. However, to approximate this, capture occasions were defined so that all parts of the study area were surveyed at least once (Figure S1). Furthermore, all calves were removed from the data set as their capture probabilities are dependent on their mothers. However, due to the gregarious nature of bottlenose dolphins, complete independence of capture probabilities to match the third assumption inherently cannot be achieved. According to Williams, Nichols, and Conroy (2002), this underestimates standard errors, but does not bias the estimates.

(4) Capturing does not alter subsequent probability of capture. Photo-identification is a noninvasive method and generally believed not to cause behavioral responses, thus the fourth assumption is satisfied.

(5) All individuals have the same probability of surviving to the next capture occasion. In bottlenose dolphins, survival can vary with age, being generally higher and less variable for adults, and thus inclusion of only adults should minimize any age-dependent effects.

(6) The sampled population is demographically closed within the primary periods. With low mortality typical for bottlenose dolphins and calculated low annual recruitment into the marked population (≈1%), these effects are unlikely to introduce significant bias (Read, Urian, Wilson, & Waples, 2003). Although temporary emigration may have occurred within primary periods, when this is random, abundance estimates are less precise, but not biased (Kendall, 1999). Therefore, violation of this assumption can be considered negligible.

2.8 | Goodness of fit testing

Even though no goodness of fit (GOF) test exists specifically for robust design models, this method is an extension of the open population Cormack-Jolly-Seber (CJS) model, hence its GOF test can be applied (Tezanos-Pinto et al., 2013, Vermeulen & Bräger, 2015). To determine if the capture-histories data from all marked adult individuals fit the fully parameterized open population CJS model, sightings were pooled by summer seasons (n = 5) and tested for goodness of fit (GOF) by running Test2 and Test3 in program U-CARE (Version 2.3.4; Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009). Only Test3.SR, which tests for effect of transient individuals, was significant ($\chi^2 = 18.74$, $df = 3$, $p < .01$). Therefore, the ad hoc solution of Pradel, Hines, Lebreton, and Nichols (1997) was used, that is, the first sightings of all marked adult individuals were removed to exclude those seen only once. The GOF test of the truncated data set revealed no effect of transience and no overdispersion, indicating good fit and confirming the use of Akaike Information Criterion statistic (AICc) appropriate for model selection.

2.9 | Estimating abundance, and apparent survival and temporary emigration rates

Pollock's Robust Design was applied to the truncated data set, in program MARK (Version 8.1; http://www.sites.warnercnr.colostate.edu/gwhite/program-mark/). Data were structured into primary and secondary periods to fit the Robust Design sampling structure (Pollock, 1982). Summer seasons when data were collected were primary periods. Secondary periods were defined by adding consecutive days of field work until all parts of the study area were surveyed at least once. This resulted in 28 secondary periods (median = 14.5 days) across 5 primary periods (Table S1).

The following parameters were estimated: φ - apparent survival – the probability of surviving to and being in the study area in the following primary period; γ'' – probability of being outside the study area during the primary period given that the individual was in the study area in the previous primary period; γ' – probability of being outside the study area during the primary period given that the individual was outside the study area in the previous primary period; N_m – abundance of marked adult individuals for each primary period. Sixteen models were constructed with the combinations of parameters φ, γ'' and γ' being either constant (.) or varying with time (t) (Table 1). Among these, two emigration patterns were modeled: (1) random emigration ($\gamma'' = \gamma'$), where the probability of being an emigrant is independent of whether the individual was an emigrant in the previous primary period, and (2) Markovian emigration ($\gamma'' \neq \gamma'$), where the probability of being an emigrant depends on whether the individual was an emigrant in the previous primary period. In four models, the terminal γ'' and γ' pairs were set to be equal ($t - 1$) to enable estimability of φ for the last interval between primary periods.

In noninvasive photo-identification studies it is generally considered that the first photographic capture does not influence the probability of subsequent captures (Fortuna, 2007; Vermeulen & Bräger, 2015). Therefore, in all models probabilities of recapture (c) were set equal to probabilities of first capture (p) and were time variant across primary and secondary periods (t).

The models estimated abundance for marked individuals only (N_m). These estimates were inflated with the proportion of marked individuals within the sample (θ) to obtain the abundance of the whole population (N_{tot}). Mean annual θ values were calculated from sightings where all present individuals were identified from Q1 and Q2 photographs. The annual abundance estimates for the whole population were then obtained using the formula:

$$N_{\text{tot}} = N_m/\theta.$$

Variance of N_{tot} was calculated according to Urian et al. (2015) as:

$$\text{var}(N_{\text{tot}}) = N_{\text{tot}}^2 \frac{\text{var}(N_m)}{N_m^2} + \frac{\text{var}(\theta)}{\theta^2}$$

TABLE 1 Pollock's Robust Design models fitted to data (rare individuals excluded). Model parameters are denoted as φ = apparent survival, γ'' = probability of emigration if the individual was present in the previous period, γ' = probability of emigration if the individual was absent in the previous period, c = first capture probability, p = recapture probability. Variability of model parameters are denoted as: (t) = time variant, (.) = constant, and ($t - 1$) = terminal parameter pair fixed.

Model	AICc	ΔAICc	AICc weights	Likelihood	Parameters	Deviance
$\{\varphi(t)\ \gamma''(.) = \gamma'(.)\ p(t) = c(t)\}$	315.70	0.000	0.262	1.000	37	1,199.125
$\{\varphi(t)\ \gamma''(.)\ \gamma'(.)\ p(t) = c(t)\}$	317.92	2.219	0.086	0.329	38	1,199.071
$\{\varphi(t)\ \gamma''(t-1)\ \gamma'(t-1)\ p(t) = c(t)\}$	317.98	2.280	0.083	0.319	39	1,196.851
$\{\varphi(.)\ \gamma''(.) = \gamma'(.)\ p(t) = c(t)\}$	317.99	2.293	0.083	0.317	34	1,208.191
$\{\varphi(.)\ \gamma''(t)\ \gamma'(.)\ p(t) = c(t)\}$	318.59	2.895	0.061	0.235	38	1,199.747
$\{\varphi(t)\ \gamma''(t)\ \gamma'(.)\ p(t) = c(t)\}$	318.62	2.919	0.060	0.232	39	1,197.49
$\{\varphi(.)\ \gamma''(t-1) = \gamma'(t-1)\ p(t) = c(t)\}$	318.83	3.132	0.054	0.208	36	1,204.523
$\{\varphi(t)\ \gamma''(.)\ \gamma'(t)\ p(t) = c(t)\}$	319.04	3.346	0.049	0.187	39	1,197.917
$\{\varphi(t)\ \gamma''(t) = \gamma'(t)\ p(t) = c(t)\}$	319.52	3.824	0.038	0.147	39	1,198.395
$\{\varphi(t)\ \gamma''(t-1) = \gamma'(t-1)\ p(t) = c(t)\}$	319.52	3.824	0.038	0.147	39	1,198.395
$\{\varphi(.)\ \gamma''(t)\ \gamma'(t)\ p(t) = c(t)\}$	319.61	3.911	0.037	0.141	39	1,198.482
$\{\varphi(.)\ \gamma''(.)\ \gamma'(.)\ p(t) = c(t)\}$	319.67	3.969	0.036	0.137	35	1,207.618
$\{\varphi(.)\ \gamma''(.)\ \gamma'(t)\ p(t) = c(t)\}$	319.68	3.978	0.035	0.136	36	1,205.369
$\{\varphi(t)\ \gamma''(t)\ \gamma'(t)\ p(t) = c(t)\}$	320.26	4.564	0.026	0.102	40	1,196.845
$\{\varphi(.)\ \gamma''(t) = \gamma'(t)\ p(t) = c(t)\}$	320.49	4.797	0.023	0.090	37	1,203.922
$\{\varphi(.)\ \gamma''(t-1)\ \gamma'(t-1)\ p(t) = c(t)\}$	320.84	5.1381	0.020	0.076	38	1,201.989

Log-normal lower and upper 95% confidence limits (LCL and UCL) for N_{tot} were calculated according to Burnham, Anderson, White, Brownie, and Pollock (1987) as:

$$\mathrm{LCL}\,(N_{\mathrm{tot}}) = N_{\mathrm{tot}}/C \quad \text{and} \quad \mathrm{UCL}\,(N_{\mathrm{tot}}) = N_{\mathrm{tot}}{*}C$$

where:

$$C = \exp\left[1.96\sqrt{\ln\left(1+\frac{\mathrm{var}(N_{\mathrm{tot}})}{N_{\mathrm{tot}}}\right)}\right]$$

2.10 | Detecting trends in abundance

To test if there was a trend in abundance, the annual abundance estimates were regressed. A slope of the regression line significantly different from zero was considered to indicate a trend (Gerrodette, 1987). Furthermore, an analysis of statistical power to detect trend in abundance was performed to identify a minimum number of years required to detect the trend observed in this study with a minimum statistical power of 0.8 (Taylor, Martinez, Gerrodette, Barlow, & Hrovat, 2007). The power analysis was performed using package "fishmethods" (Gary, 2015) in R (R Core Team, 2016), with significance level set to 0.05, type of change in abundance set to linear, test type set to one-tailed, and using *CV* value averaged from the annual *CV* values from abundance estimates.

2.11 | Fertility and offspring survival rates

The annual fertility rates were calculated as the number of newborns in a year divided by the number of females known to be alive in that year. The intercalving interval was calculated as the inverse of the mean of the annual fertility rates (Fortuna, 2007).

To estimate calf survival rates, Cormack-Jolly-Seber models adapted for age-dependent variability in survival rates (Lebreton, Burnham, Clobert, & Anderson, 1992) were applied to the sample of calves born during the study period to the mothers seen in all 5 years of the study. The survival rates were modeled for up to age 4 and different combinations of pooled ages. As only calves born to mothers seen in each year were selected and assuming that mothers' and calves' capture probabilities are the same, the capture probabilities were fixed at 1.

3 | RESULTS

3.1 | Research effort and photo-identification

The research effort amounted to 13,896 km and varied among months, with the highest being achieved in June, July, and August (Table 2). Twelve fish farms were checked for presence of dolphins 197 times and operating trawlers 25 times. A total of 284 sightings were recorded, of which 192 were "on effort," 56 were "FF sightings," 1 was a "TW sighting," and 35 were "off effort sightings." Locations of sightings and spatial distribution and density of research effort are shown in Figure 2.

A total of 336 individuals were identified during the study period, of which 255 were marked (D1 or D2 distinctiveness classes), i.e., considered reliably identifiable. Of these, 75 were females, 14 males, and 166 of unknown sex.

TABLE 2 Number of kilometers surveyed "on effort" and number of sightings per year, month, and total.

Year	May	June	July	August	September	October	Total
Kilometers on effort							
2013		533	675	814	679		2,701
2014		641	837	649	552	182	2,861
2015	77	490	951	1,172	94		2,784
2016		638	892	842	762	88	3,222
2017	393	687	577	584	87		2,328
Total	470	2,989	3,932	4,061	2,174	270	13,896
Sightings							
2013		12	13	13	15		53
2014		12	18	8	7	2	47
2015	2	6	26	38	5		77
2016		5	18	16	16	2	57
2017	17	9	8	15	1		50
Total	19	44	83	90	44	4	284

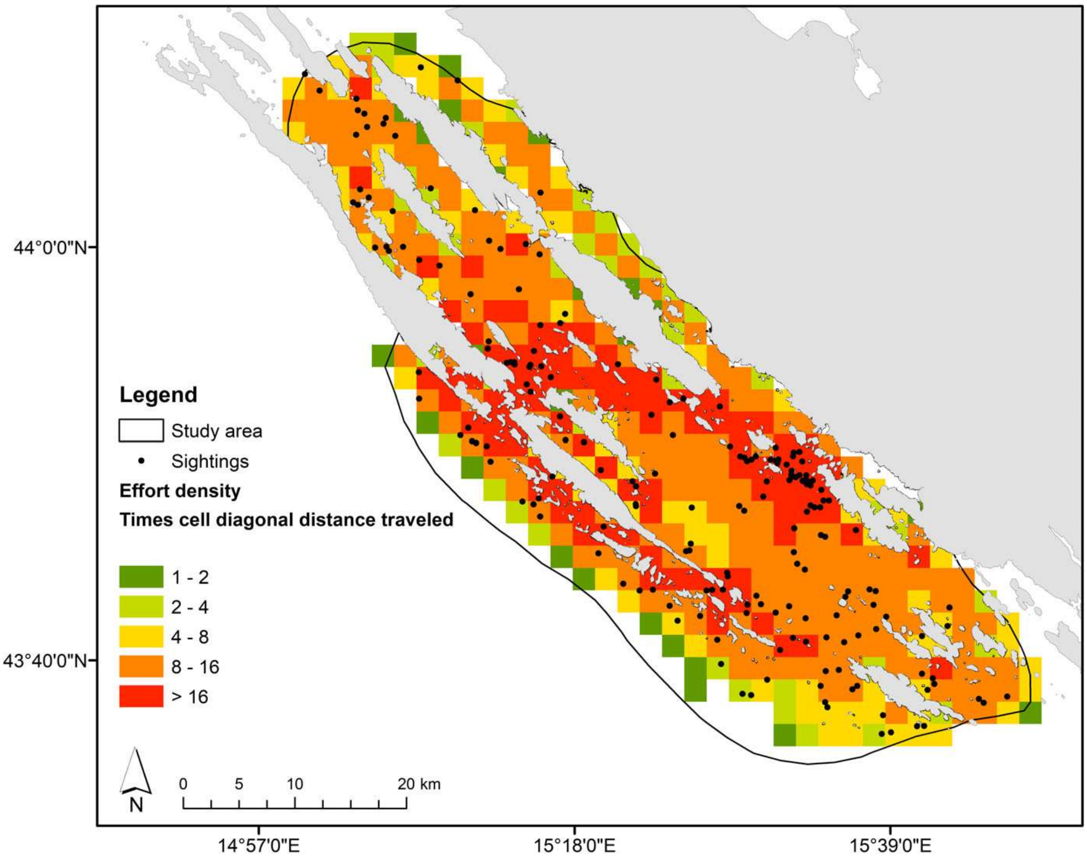

FIGURE 2 Spatial distribution and density of research effort expressed as number of times the distance equal to cell diagonal was travelled on effort in each 2 × 2 km^2 grid cell. Black dots represent locations of all recorded sightings (N = 284).

The discovery curve showed steepest growth in the first 2 years of study and slower growth afterwards, but did not reach plateau for marked and all individuals. The curve for regular and occasional individuals reached plateau at the third year of study (Figure 3).

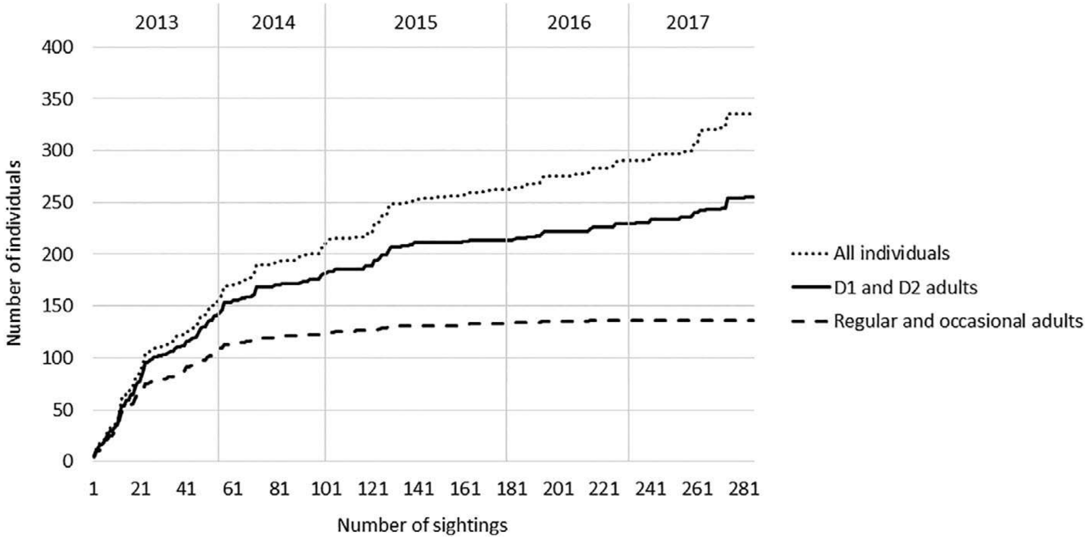

FIGURE 3 Discovery curves for all individuals (*N* = 336, dotted line), only marked (D1 and D2) adults (*N* = 255, black line), and regular and occasional adults (*N* = 136, dashed line).

3.2 | Group sizes

The mean annual group sizes varied from 5.73 (*SE* = 0.42) in 2015 to 7.46 (*SE* = 0.88) in 2017 and were not found to be significantly different between years (ANOVA, *F* = 1.573, *df* = 4, *p* = .182) (Kruskal-Wallis, χ^2 = 4.91, df = 4, *p* = .297). There was a significant difference (Kruskal-Wallis, χ^2 = 65.6, *df* = 1, $p < .01$) in sizes of groups composed of adults only ($\bar{x}$= 4.56, *SE* = 0.26) and those with nonadult individuals present ($\bar{x}$ = 8.53, *SE* = 0.42). No significant difference in size could be found (Kruskal-Wallis, χ^2 = 27.0, *df* = 1, *p* = .26) between groups at the fish farms ($\bar{x}$ = 6.60, *SE* = 0.52) and nonfish farm groups ($\bar{x}$= 6.88, *SE* = 0.31).

3.3 | Site fidelity

Mean annual sighting rate for the 255 marked individuals was 0.45 (*SE* = 0.020). Based on the annual sighting rate, 89 (34.9%) individuals were classed as "regular," 47 (18.4%) as "occasional," and 119 (46.7%) as "rare." Of the 119 rare individuals, 9 were known former calves that recruited into sample by becoming adult and marked. Of all rare individuals, 85 (71.4%) were seen only once, indicating that most of these individuals remained in the study area only briefly.

3.4 | Group encounter rates

The average group encounter rate for the whole study period was 1.501 groups/100 km (*SE* = 0.160). Annual group encounter rates ranged from 1.159 groups/100 km (*SE* = 0.239; 2014) to 1.942 groups/100 km (*SE* = 0.329; 2015) (Figure 4). No significant differences in group encounter rates between years could be determined with Kruskal-Wallis test (*H* = 3.002, *df* = 4, *p* = .558).

The Moran's *I* index showed a significant spatial autocorrelation between cells used in this analysis (*I* = 0.081, z = 2.097, *p* = .036).

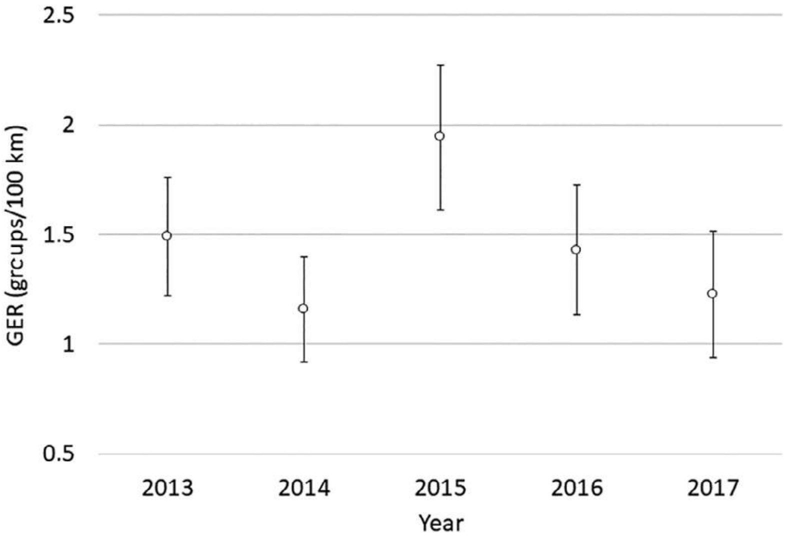

FIGURE 4 Annual group encounter rates expressed as number of groups per 100 km surveyed on effort. Vertical bars represent standard errors.

TABLE 3 Estimated apparent survival rates (φ) for regular and occasional marked adult individuals, between years with 95% confidence intervals (CI) and standard errors (*SE*).

Years	φ (95% CI)	*SE*
2013–2014	0.986 (0.047–0.999)	0.051
2014–2015	0.911 (0.689–0.979)	0.063
2015–2016	0.737 (0.602–0.839)	0.061
2016–2017	0.958 (0.031–0.999)	0.133

3.5 | Apparent survival and temporary emigration rates

Using the truncated data set, i.e., with the first sightings eliminated, 176 individuals were included in the Robust Design analysis. The best-fitting model (Table 1) suggested time-variant apparent survival rates (Table 3) and time-invariant and random temporary emigration rate of 0.172 (95% CI 0.089, 0.307). Even though other models had some support from the data, their AICc weights were three or more times lower than the best-fitting model (Table 1).

3.6 | Trends in abundance

The abundance estimates for the marked population ranged from 94 individuals in 2016 to 116 individuals in 2015 (Table 4). When corrected for the proportion of marked individuals (θ), the abundance of the whole population varied annually, from 116 individuals (95% CI 107, 133) in 2016 to 138 individuals (95% CI 121, 165) in 2015 (Table 4).

A *z* test found no significant difference between annual estimates. The regression of annual abundance estimates revealed a negative slope of 11.4% overall and 2.9% annually, but the significance could not be confirmed ($R^2 = 0.386$, $t = -1.374$, $p = .26$; Figure 5).

Using the *CV* values averaged across years (*CV* = 0.092), the statistical power to detect the negative change in abundance as indicated by the regression was below the 0.8 threshold conventionally considered as acceptable. A further 27 years would be required to detect a decline of this magnitude with the power of ≥0.8 and the current study design and average *CV* values.

TABLE 4 Number of secondary occasions and regular and occasional marked adult individuals captured per primary occasion (summer seasons), estimates of annual abundance for marked adult individuals (N_m) and whole population (N_{tot}), with 95% confidence intervals (CI) and standard errors (*SE*), and proportion of marked individuals (θ).

Year	Secondary periods	Marked individuals captured	N_m	*SE* (N_m)	95% CI (N_m)	θ	N_{tot}	95% CL (N_{tot})	*SE* (N_{tot})	CV
2013	6	88	111	7.679	100–132	0.84	132	119–157	11.569	0.087
2014	6	83	105	6.967	95–123	0.85	124	112–145	10.565	0.085
2015	6	84	116	9.176	102–139	0.84	138	121–165	13.707	0.099
2016	6	81	94	5.049	87–108	0.81	116	107–133	8.281	0.071
2017	4	74	103	9.161	90–127	0.88	117	102–144	13.660	0.116

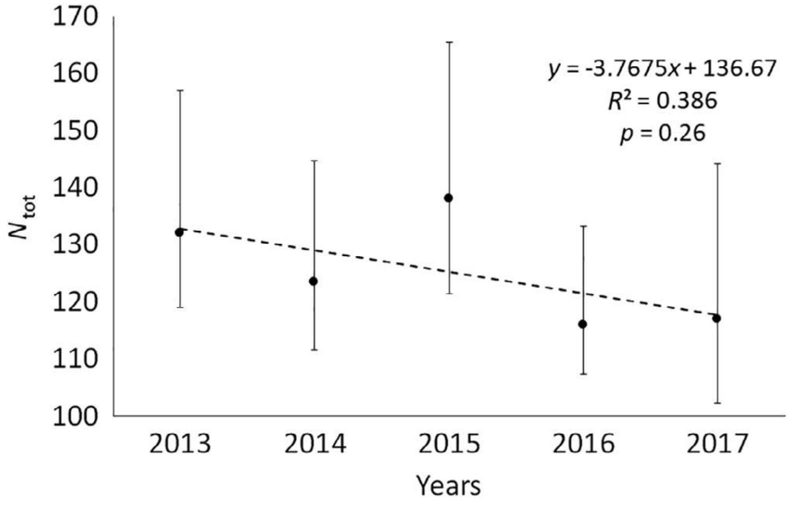

FIGURE 5 Annual estimates of abundance of regular and occasional adult individuals, corrected for the proportion of unmarked individuals. Vertical lines represent 95% confidence intervals. Regression line shows decline, but significance could not be determined.

TABLE 5 Age-dependent Cormack-Jolly-Seber models for estimation of calf survival, ranked by the AICc values. Only models with sufficient support from data (ΔAICc values <2) are shown. φ = apparent survival, *p* = capture probability, Age = survival parameters grouped by age, *t* = time dependent parameters, (.) = time independent parameters.

	Model	AICc	ΔAICc	AICc weight	Parameters	Deviance
1C	Φ[Age1–2(.)] φ[Age ≥3(.)] *p*(.)	28.0626	0	0.31127	2	6.5217
2C	φ(Age1) φ(Age2) φ[Age ≥3(.)] *p*(.)	28.4449	0.3823	0.25711	3	4.4765
3C	Φ[Age1–3(.)] φ[Age4(.)] *p*(.)	28.5133	0.4507	0.24847	2	6.9724
4C	φ(t) *p*(.)	29.1234	1.0608	0.18314	4	2.5539

3.7 | Fertility rate and calf survival

During the study period, a total of 93 young individuals (newborns and calves) associated with 66 females were observed. Of these, 28 were born during the study period and 22 were observed to survive to become independent. The annual fertility rate varied from 0.02 to 0.228, with a mean of 0.171 (*SE* = 0.038). The intercalving interval, expressed as inverse of fertility rate, was 5.83 years. The number of females with 2 observed births during the study period was insufficient to calculate the average intercalving interval from direct observations.

TABLE 6 Estimates of apparent survival of calves (φ) with standard errors (*SE*) and 95% confidence intervals (CI) from models with support from data (ΔAICc <2). Age 2 in models 2C and 4C, and Age ≥3 in models 3C and 4C could not be estimated.

Model	Parameter	Estimate	*SE*	95% CI
1C	Φ Age 1–2	0.9231	0.0523	0.7393–0.9807
	Φ Age ≥3	0.5714	0.1870	0.2298–0.8563
2C	Φ Age 1	0.8750	0.0827	0.6140–0.9686
	Φ Age 2	N/A	N/A	N/A
	Φ Age ≥3	0.5714	0.1870	0.2298–0.8563
3C	Φ Age 1–3	0.8750	0.0585	0.7106–0.9523
	Φ Age 4	N/A	N/A	N/A
4C	Φ Age 1	0.8750	0.0827	0.6140–0.9686
	Φ Age 2	N/A	N/A	N/A
	Φ Age 3	0.6667	0.1925	0.2681–0.9161
	Φ Age 4	N/A	N/A	N/A

Nineteen calves were born to 16 females seen in all 5 years so that their fate was known. Of these, two (10.53%) were presumed to have died before age of 1 as they were seen as newborn in one summer only. Four age-dependent CJS models applied to capture histories of these 19 calves had support from data (AICc <2) (Table 5). The apparent survival probabilities estimated by these models for various age groups are shown in Table 6.

4 | DISCUSSION

4.1 | Site fidelity

Based on our results and our definitions, the study area hosts a mixture of regular, occasional, and rare animals. More than half of all marked adults were seen in at least 2 years. The discovery curve indicated that the majority of regular and occasional individuals had been encountered by the third year of the study. However, despite reduced growth in the last 3 years, the curve for both marked and all individuals did not reach asymptote. This may be explained by encounters of rare new individuals and recruitment from the community of regular individuals. Furthermore, some of those classed as occasional and rare may actually be regular individuals, but were seen only in one or two years due to variability in capture probabilities. Additional years of field work are needed to provide more robust insight into the site fidelity of bottlenose dolphins in North Dalmatian waters, preferably with extension of research effort in winter months to clarify whether the site fidelity patterns are maintained year-round.

Bottlenose dolphin populations exhibit various degrees of site fidelity in relation to habitat characteristics (Campbell, Bilgre, & Defran, 2002; Connor et al., 2000). As a general trend, open or oceanic habitats promote wider ranging behavior, resulting in lower site fidelity to certain areas, whereas complex or enclosed coastal habitats with temporally and spatially predictable food sources promote higher fidelity to relatively small areas (Gowans, Würsig, & Karczmarski, 2007). Our study area can be seen as encompassing both habitat types. In fact, the majority of the rare individuals were encountered south-west of the outer stretch of islands, a portion of the study area that can be described as an open habitat. Although definitions of regular vs. rare individuals, or residents vs. transients when actual residency can be established, vary among studies, the link between site fidelity and habitat characteristics was found in other studies. For instance, populations in open habitats off Sicily (Papale et al., 2017) and in the Madeira Archipelago (Dinis et al., 2016) comprised a low proportion of residents, while studies in the enclosed Amvrakikos Gulf, Greece (Bearzi, Agazzi, Bonizzoni, Costa, & Azzellino, 2008a; Gonzalov et al., 2016) and Sado Estuary, Portugal (Augusto, Rachinas-Lopes, & dos Santos, 2012) found a high degree of site fidelity for the local communities. In the eastern Adriatic Sea, and using the same arbitrary criteria as in this study (observed in 1 year only), 56% of all identified individuals in the island of Vis area were rare (Holcer, 2012), whereas in Slovenian and adjacent waters 48% of individuals were rare (Genov, Kotnjek, Lesjak, Hace, & Fortuna, 2008).

4.2 | Group sizes and encounter rates

Small mean group sizes, as found in this study (5.73–7.46), are typical for coastal areas (Bearzi, Fortuna, & Reeves, 2008b; Fortuna, 2007). Different factors have been proposed to influence the group size in bottlenose dolphins, including optimization of foraging efficiency and predation risk (Campbell et al., 2002). So far, no evidence of shark predation on dolphins exists in the eastern Adriatic. Therefore, small group sizes observed in this study may be explained as an adaptation to prey scarcity in the area (Dulčić et al., 2005) by reducing competition among conspecifics in foraging groups (Kerr, Defran, & Campbell, 2005). Groups with newborns and calves were significantly larger than groups composed of adult individuals only. The same pattern was described in other eastern Adriatic regions (Bearzi, Notarbartolo Di Sciara, & Politi, 1997; Holcer, 2012) and in other bottlenose dolphin populations (Barker & Berrow, 2016; Rogers, Brunnick, Herzing, & Baldwin, 2004). Larger group size may be beneficial to nursing mothers and their calves through alloparental care, enhanced protection and increased knowledge transfer to young individuals (Johnson & Norris, 1986). Fish farms present patches of concentrated prey and are known to attract bottlenose dolphins (Pace, Pulcini, & Triossi, 2012), thus an effect on group size could be expected. However, this could not be confirmed in this study, indicating that factors other than prey availability alone may influence the size of groups feeding at the fish farms. For instance, fish farms may influence social structure (Pace et al., 2012), which consequently may affect group sizes. However, further research and detailed analysis of social dynamics in relation to fish farms is required to better understand effects of aquaculture on bottlenose dolphin grouping patterns in North Dalmatia.

The annual group encounter rates were relatively stable across the five summer seasons included in this study. However, the Moran's I index suggested that group encounter rates in grid cells were spatially autocorrelated. This is indicative of uneven habitat use pattern, as would be expected in a habitat with diverse physiographic and anthropogenic features. Avoidance of areas with intense boat traffic and related underwater noise (Rako et al., 2013a), and preference for aquaculture sites (Bearzi et al., 2008b) may explain local differences in dolphin occurrence. To fully understand what effect the local environmental and anthropogenic factors have on the spatial ecology of bottlenose dolphins in North Dalmatia, a detailed habitat use analysis is needed.

4.3 | Temporary emigration patterns, apparent survival and abundance

As the majority of rare individuals were removed with the *ad hoc* method of Pradel et al. (1997), it must be noted that the estimates obtained from Robust Design models pertain primarily to individuals classed as regular or occasional in north Dalmatian waters. According to Pradel et al., (1997), this solution results in higher standard errors, but the estimates remain unbiased.

The best-fit model indicated a random and constant temporary emigration pattern. Temporary emigration rate was generally comparable to those estimated for other coastal populations, for instance, 0.08–0.30 in the adjacent Kvarner region (Fortuna, 2007), 0.16 in Gulf of Corinth, Greece (Santostasi et al., 2016), and 0.18–0.82 in Bay of Island, New Zealand (Tezanos-Pinto et al., 2013).

The apparent survival rates varied among years, from 0.737 (*SE* = 0.061) in 2016 to 0.986 (*SE* = 0.051) in 2014. In long-living species, such as bottlenose dolphins, the apparent survival rates are typically above 0.9 (Nicholson, Bejder, Allen, Krützen, & Pollock, 2012; Vermeulen & Bräger, 2015). In this study, the lowest value of apparent survival rate for adults (in 2016) is among the lowest obtained for bottlenose dolphins and similar only to those found in the Gulf of Corinth (Santostasi et al., 2016). In Robust Design models permanent emigration and mortality are confounded. Considering that the temporary emigration rate estimated in this study was 0.172, the relatively low apparent survival rate in 2016 may thus be biased downwards (Santostasi et al., 2016).

The estimated abundance for the resident and occasional bottlenose dolphins inhabiting the North Dalmatian waters varied among years between 116 individuals in 2016 (95% CI = 107–133), and 138 individuals in 2015 (95% CI = 121–165). These estimates are similar to other coastal communities, which rarely exceed a few hundred (Bearzi et al., 2008a; Bouveroux, Tyson, & Nowacek, 2014; Kerr et al., 2005). In the eastern Adriatic, the resident community inhabiting the 1,500 km^2 Kvarner region was estimated to be around 200 individuals, with interannual variations (Pleslić et al., 2015). The community inhabiting 1,000 km^2 of Slovenian and adjacent waters was estimated to be 68 individuals (Genov et al., 2008), while the one around the island of Vis was around 400 individuals, albeit in a much larger area of 7,400 km^2 (Holcer, 2012).

4.4 | Trend in abundance

The negative slope of the regression of annual abundance estimates was not statistically significant. Nevertheless, it calls for attention, as small natural variations in population size are difficult to distinct from real trends (Gerrodette, 1987). Therefore, we consider two scenarios.

In the first scenario, the observed changes in abundance are attributable to natural variations. Mark-recapture studies are sensitive to photographic effort intensity and coverage of the study area (Parra et al., 2006). In the present study the overall annual research effort was consistent from 2013 to 2016 and somewhat lower in 2017 (Table 2). Furthermore, secondary occasions were carefully selected to maintain consistency in terms of area coverage. Given that the local resident community was not closed to migrations (Pleslić et al., 2019), the differences in annual abundance estimates likely reflect interannual variations in ranging patterns, rather than inconsistent effort or actual changes in abundance. This is further supported by the stability of group encounter rates across years.

In the second scenario, the North Dalmatian community went through a decline of 11% over 5 years. Even though relatively high precision of abundance estimates was achieved, the statistical power to detect this change was below 0.8, a value conventionally considered as a threshold to reliably confirm a decline (Taylor, Martinez, Gerrodette, Barlow, & Harvot, 2007), and it would take 27 years to detect this decline with the survey design described here. Nevertheless, besides the precision of abundance estimates and duration of study, the ability to detect trends in abundance also depends on the rate of change in population size (Gerrodette, 1987). Continuous monitoring is therefore recommended to enable detection of a trend, should the North Dalmatian community experience a dramatic change in size.

4.5 | Fertility and calf survival

The fertility rate and the related intercalving interval are among primary descriptors of female reproductive success, particularly for long-lived and slowly reproducing species (Rossi et al., 2017). Due to extensive time spans needed to obtain these parameters, available data are limited, particularly for the Mediterranean populations. Here, the duration of the study prevented from having a sample large enough to calculate the intercalving interval directly and the results should therefore be considered as potentially biased. The fertility rate (0.171, *SE* = 0.038) was variable among years, and comparable to that found by Fortuna (2007) in the adjacent Kvarnerić region (0.171, *SE* = 0.046), using the same methodology. In the Eastern Ligurian Sea and using a longer time span, Rossi et al. (2017) reported considerably higher fertility rates, ranging between 0.290 and 0.407. Differences in reproductive success among populations have been proposed to be caused by environmental and social factors, and demographic plasticity of the species (Fruet, Genoves, Möller, Botta, & Secchi, 2015; Whitehead & Mann, 2000).

The age-adapted CJS models that distinguished the survival probabilities between the first three years of life (models 2C and 4C) estimated the first-year survival to 0.875 (95% CI = 0.614–0.968). This estimate is marginally higher than those found along the east coast of Scotland (0.865; Arso Civil et al., 2019), in the Sarasota Bay, Florida (0.811; Wells & Scott, 1990), Doubtful Sound, New Zealand (0.862; Currey et al., 2009), and around Mikura island, Japan (0.866; Kogi, Hishii, Imamura, Iwatani, & Dudzinski, 2004). In the adjacent Kvarner region the first-year survival was notably lower (0.771; Fortuna, 2007). Two out of 19 newborns (10.53%) died before reaching age 1, which is close to model estimates (Table 6, models 2C and 4C). In bottlenose dolphins living in temperate seas with seasonal differences in temperature, peaks in calving season occur in warm summer months (Henderson, Dawson, Currey, Lusseau, & Schneider, 2014; Robinson et al., 2017; Vermeulen & Bräger, 2015). The present study encompassed summer months only. However, the same pattern of birth seasonality was observed in the adjacent Kvarner area (Bearzi et al., 1997). Considering the ecological similarities of the two areas it is reasonable to expect such seasonality to exist also in the North Dalmatian community. In that case, the number of calves born and died before annual field work began and the resulting upward bias in the first-year survival rate should be low. The probability of survival to age 3 and older was comparably low and had low precision in all models. This age group coincides with the average age of weaning (Mann, Connor, Barre, & Heithaus, 2000) when calves may emigrate or rapidly change dorsal fin markings, making re-identification impossible. As these factors are confounded with real mortality, the estimated survival for age ≥ 3 is negatively biased. The same bias in estimating the apparent survival probability of older calves was found by Arso Civil et al. (2019). Furthermore, as the calf survival was analyzed based on newborns of females seen in all years of study these results are indicative only of the regular proportion of the local community.

4.6 | Conservation implications

This is the first study to describe occurrence and demographic parameters of the bottlenose dolphin community inhabiting the waters of North Dalmatia. As such, it provides baseline information in support of conservation measures and benchmark for future monitoring, particularly to detect any trend in abundance and to further explore reproductive capacity. The two Sites of Community Importance (SCI) for bottlenose dolphins currently in place under the Natura 2000 scheme cover 44% of the North Dalmatian community home range (Figure 1; Pleslić et al., 2019). To comply with the European Union Habitat Directive which requires ensuring favorable ecological conditions for survival of the local bottlenose dolphin community (Council Directive 92/43/EEC; Council of the European Communities), conservation measures within these SCIs will have to target those anthropogenic factors in the area that are recognized as having a detrimental effect on bottlenose dolphins: prey depletion, fisheries interactions, and marine traffic through physical and acoustic disturbance (Bearzi et al., 2008b; Bejder et al., 2006; Rako et al., 2013b).

With low productivity and high fisheries pressure, waters of North Dalmatia are overfished (Dulčić et al., 2005). In such conditions, their opportunistic nature enables bottlenose dolphins to exploit alternative prey sources, e.g., fish farms (Pace et al., 2012), bottom trawlers (Fertl & Leatherwood, 1997), and depredation on bottom nets (Bearzi et al., 2008b; Brotons, Grau, & Rendell, 2008). These interactions with fisheries may, however, lead to incidental mortality (Díaz López, 2006) or deliberate retaliatory killing (Bearzi et al., 2008b). During this study, one newborn was observed entangled in a rope of an unidentified fishing gear and was presumed to have died as a consequence, because the mother was seen alone 2 weeks afterwards. Furthermore, one case of intentional injuring (shot with a spear-gun harpoon) was recorded. The magnitude and effects of these interactions at population level remain unknown.

Intense marine tourism in the summer and particularly the recently emerging dolphin-watching tours focusing on areas around the fish farms with highest occurrence of dolphins, expose the North Dalmatian bottlenose dolphin community to physical harassment and underwater acoustic disturbance. The physical presence of boats may induce both short-term and long-term displacements from the affected areas (Bejder et al., 2006; Rako et al., 2013a), whereas underwater noise may have adverse effects by masking biologically relevant information, leading to reduced communication and foraging efficiency (Rako et al., 2013b). It is therefore important to direct conservation measures at minimizing physical and acoustic disturbance from boats. Speed limitations and a code of conduct in presence of dolphins, implemented through a legal framework and promoted through public awareness campaigns may help alleviate these threats.

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AUTHOR CONTRIBUTIONS

Grgur Plesli: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Visualization, Writing-original draft. **Nikolina Rako-Gospić:** Data curation; project administration; supervision; validation; writing-review and editing. **Draško Holcer:** Conceptualization; funding acquisition; resources; supervision; writing-review and editing.

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ENDNOTE

[1] http://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=HR3000426
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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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Appendix S1. A detailed overview of distances traveled „on effort“, and spatial and temporal distribution of „on effort“ survey tracks per each secondary period.

Table S1. Distances traveled „on effort“, and duration of each secondary period used for the Robust Design modelling

Period Primary_Secondary	Effort (km)	From date	To date
2013_1	405	6.6.2013	17.6.2013
2013_2	405	18.6.2013	15.7.2013
2013_3	421	17.7.2013	29.7.2013
2013_4	462	1.8.2013	13.8.2013
2013_5	409	14.8.2013	4.9.2013
2013_6	649	5.9.2013	26.9.2013
2014_1	459	4.6.2014	12.6.2014
2014_2	527	26.6.2014	7.7.2014
2014_3	490	8.7.2014	24.7.2014
2014_4	483	1.8.2014	12.8.2014
2014_5	489	24.8.2014	9.9.2014
2014_6	409	17.9.2014	4.10.2014
2015_1	489	12.6.2015	28.6.2015
2015_2	400	2.7.2015	5.7.2015
2015_3	487	16.7.2015	28.7.2015
2015_4	447	30.7.2015	8.8.2015
2015_5	438	13.8.2015	28.8.2015
2015_6	409	29.8.2015	2.9.2015
2016_1	528	7.6.2016	26.6.2016
2016_2	660	30.6.2016	11.7.2016
2016_3	527	25.7.2016	5.8.2016
2016_4	588	10.8.2016	29.8.2016
2016_5	501	31.8.2016	14.9.2016
2016_6	487	23.9.2016	1.11.2016
2017_1	605	19.5.2017	10.6.2017
2017_2	474	20.6.2017	29.6.2017
2017_3	743	11.7.2017	4.8.2017
2017_4	505	19.8.2017	4.9.2017

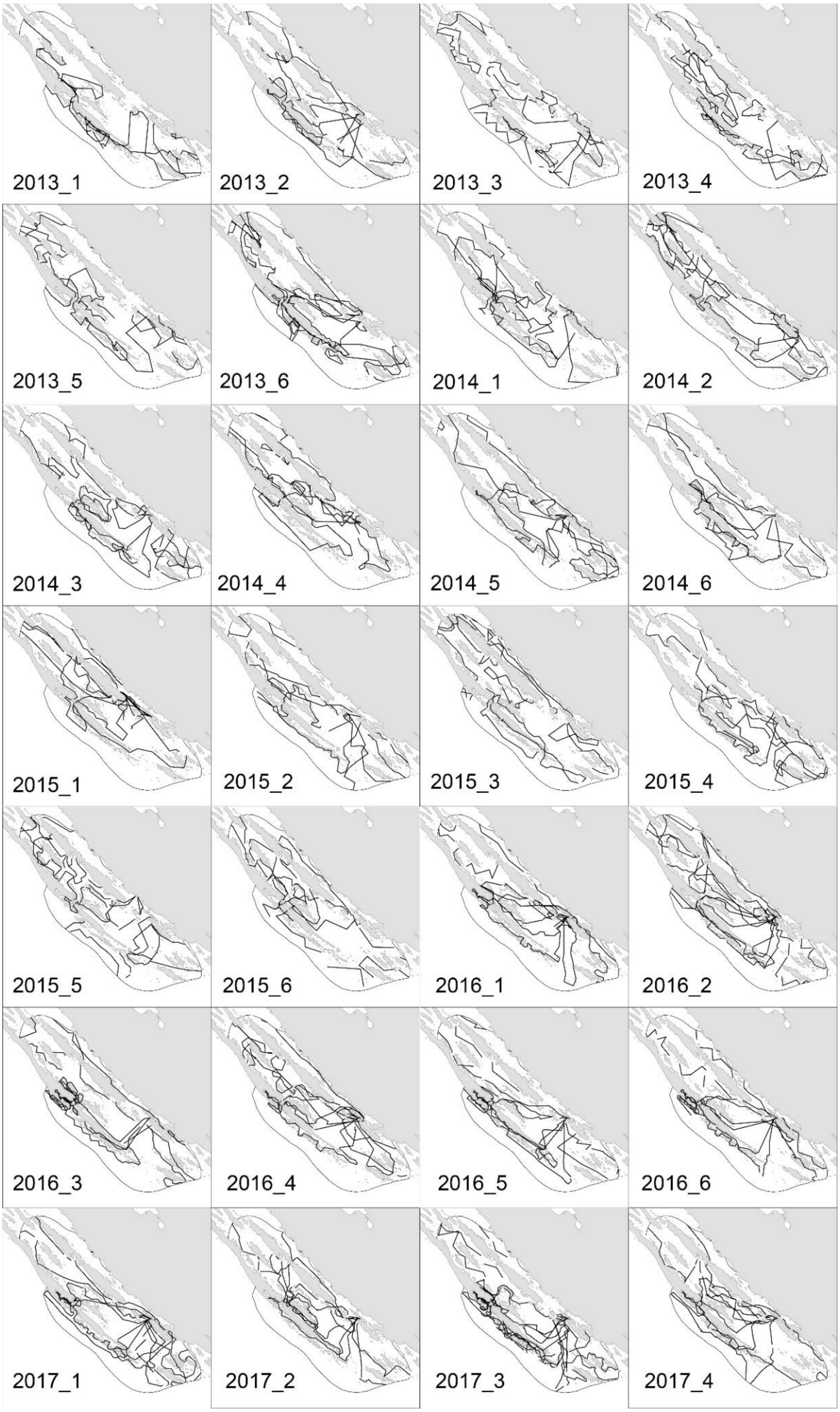


Figure S1. Spatial distribution of surveys across the 28 secondary periods.

4. RASPRAVA

4.1. Struktura populacije dobrih dupina

Prostorna i društvena struktura dobrih dupina duž istočne obale Jadrana opisane su u znanstvenom radu **1**. Rezultati ukazuju na postojanje tri društvena klastera u području od akvatorija otoka Cresa do akvatorija otoka Visa. S obzirom da je utvrđeno da su jedinke značajno snažnije društveno povezane s jedinkama iz istog klastera nego onima iz ostatka populacije, tri utvrđena društvena klastera mogu se smatrati zajednicama prema definiciji od Croft i sur. (2008). Rezultati analize područja obitavanja identificiranih zajednica pokazuju da su one i prostorno odvojene. Tri identificirane zajednice nazvane su po područjima u kojima većinom borave: Kvarnerić (K), Sjeverna Dalmacija (ND) i Vis (V) (znanstveni rad **1**; Slika 10). Ovime rezultati znanstvenog rada **1** potvrđuju pretpostavku o postojanju zasebnih zajednica duž istočne obale Jadrana temeljenu na ranijim usporedbama kataloga leđnih peraja iz različitih područja istraživanja, te prvi put utvrđuju područja obitavanja lokalnih zajednica. U ranije provedenim istraživanjima, lokalna zajednica dobrih dupina u Kvarneriću opisana je kao rezidentna i relativno zatvorena (Bearzi i sur. 1997; Fortuna 2006; Pleslić i sur. 2015), no u sva tri navedena istraživanja autori su pretpostavili da je područje obitavanja ove zajednice veće od onoga obuhvaćenog područjem istraživanja. Slično tome, veća područja obitavanja od onih obuhvaćenih istraživanjima provedenima u Murterskom moru i NP Kornati pretpostavile su i Impetuoso i sur. (2003) i Kammigan i sur. (2008). Istraživanjem u području otoka Visa utvrđena su područja obitavanja jedinki MCP metodom, no analiza područja obitavanja zajednice nije provedena (Holcer 2012).

Treba naglasiti da je utvrđivanje društvene strukture i područja obitavanja zajednica, radi zahtjeva metode, vršeno na uzorku jedinki opaženih 10 ili više puta tijekom istraživanja, odnosno jedinki koje se mogu smatrati privrženima području istraživanja. U područjima obitavanja triju zajednica zabilježen je i značajan broj jedinki koje pokazuju nisku razinu privrženosti području (znanstveni radovi **1** i **3**), a što je opisano i u ranijim istraživanjima u područjima Kvarnerića (Pleslić i sur. 2015) i otoka Visa (Holcer 2012). Ipak, kada se uzmu u obzir i ove jedinke, ukupan broj migracija među područjima obitavanja zajednica i dalje je nizak, a vjerojatnost da jedinke ostanu u području obitavanja zajednice je značajno viša od vjerojatnosti da migriraju u područje obitavanja druge zajednice ili neko drugo područje (znanstveni rad **1**). Stoga se nameću dva zaključka. Prvi je da su lokalne, priobalne zajednice utvrđene ovim radom međusobno slabo povezane, a da se glavnina interakcija događa sa jedinkama koje obitavaju u područjima koja nisu obuhvaćena ovim radom. Ovo upućuje na važnost proširenja područja istraživanja u dijelove otvorenog mora Jadrana kako bi se bolje razumjeli ekološki odnosi priobalnih, rezidentnih zajednica sa onima iz otvorenog mora. Drugi je da utvrđena područja obitavanja zajednica nisu odraz prostorne distribucije istraživačkog napora, već dobro odražavaju stvarna područja koja te zajednice redovno koriste, te time predstavljaju polaznu informaciju za daljnja istraživanja (npr. korištenje informacije o području obitavanja pri modeliranju demografskih parametara; znanstveni rad **3**) i za osmišljavanje mjera zaštite.

Činjenica da dobri dupini u ovome i brojnim drugim istraživanjima u priobalnim područjima pokazuju sličnost u smislu da postoje zasebne zajednice s više ili manje definiranim područjem obitavanja, ali da u pravilu te zajednice nisu u potpunosti izolirane, nameće dva pitanja: a) koji čimbenici kod dobrih dupina dovode do privrženosti području obitavanja unatoč činjenici da je vrsta sposobna prevaljivati velike udaljenosti u kratkom vremenu, i b) koji čimbenici uzrokuju povremena napuštanja područja obitavanja.

Prema Nekolny i sur. (2017), ukoliko stanište to omogućava, dobri dupini mogu zadovoljiti osnovne potrebe u relativno malom prostoru u kojem posljedično provode većinu vremena. Ovo dovodi do adaptacije na lokalne ekološke uvjete što rezultira formiranjem zajednica specijaliziranih za određeni tip staništa, odnosno resurse koje to stanište pruža (Wiszniewski i sur. 2010). Ovakvo strukturiranje u zajednice događa se i na relativno malim područjima, ukoliko su razlike među staništima dovoljno izražene. Tako su u zaljevu Port Stephens (Australija), u rasponu od 20 km, opisane dvije zajednice od kojih se jedna zadržava u zapadnom dijelu kojeg karakteriziraju odlike estuarija, dok druga obitava u istočnom dijelu koji je tipično morsko stanište (Wiszniewski i sur. 2009). Razlike među dostupnim lokalnim resursima između pojedinih područja dovode i do specijalizacije u tehnikama lova (Fertl i Leatherwood 1997; Díaz López 2006), a koje se prenose među jedinkama horizontalno procesom „društvenog učenja“ (Mann i sur. 2012), te vertikalno sa ženki na mladunce (Krützen i sur. 2005). Vertikalni prijenos sa ženki na mladunce naročito je značajan jer za posljedicu ima dva učinka koja doprinose njihovom ostanku u određenom području obitavanja. Prvo, ženke za vrijeme brige o mladuncu iskorištavaju prednost poznavanja područja, odnosno specijalizirane tehnike lova, radi lakšeg zadovoljavanja povišenih energetskih zahtjeva, te prednost koju pruža poznavanje ostalih pripadnika zajednice radi pomoći u brizi o i zaštiti mladunca (Connor i sur. 2000). Drugo, ženke i druge jedinke iste zajednice kroz proces društvenog učenja prenose specijalizirane tehnike lova na mladunce, čime doprinose njihovoj natalnoj filopatriji (Tsai i

Mann 2013). I u ovome radu zabilježena je natalna filopatrija u području Kvarnerića (znanstveni rad **2**), no radi relativno malog uzorka utvrđivanje njenog značaja na razini cijele zajednice nije bilo moguće. Nadalje, postoje i razlike u fiziografskim i antropogenim obilježjima područja obitavanja zajednica K, ND i V, a koje mogu dovesti do adaptacije na lokalne uvjete (Wiszniewski i sur. 2010) i posljedično privrženosti području obitavanja utvrđene u znanstvenom radu **1**. Tako se područja Kvarnerića i sjeverne Dalmacije mogu opisati kao plitka i zatvorena, dok se područje otoka Visa može opisati kao otvoreno stanište s većim dubinama. Osim toga, primjetne su razlike u broju ribogojilišta (Kvarnerić: 2, sjeverna Dalmacija: 12, Vis: 0) i intenzitetu koćarenja među ovim područjima (Tablica 1).

Povremena napuštanja područja obitavanja kakva su zabilježena u ovome radu (znanstveni rad **1**) opisana su i u drugim istraživanjima dobrih dupina u Sredozemnom moru (Gnone i sur. 2011), Crnom moru (Gladilina i sur. 2016), ali i kod ostalih vrsta roda *Tursiops* (Möller i sur. 2002). Više je mogućih razloga ovakvoga ponašanja. Kod dobrih dupina, kao i drugih sisavaca, mužjaci mogu napuštati područje obitavanja radi traženja ženki dostupnih za parenje (Bearzi i sur. 2011), čime se smanjuje i vjerojatnost parenja među srodnicima (Dobson i Jones 1985). Uslijed povremene smanjene dostupnosti plijena u području obitavanja radi smanjenja kompeticije jedinke moraju plijen tražiti drugdje (Bearzi i sur. 2008). Također, sezonske varijacije u intenzitetu antropogenih čimbenika poput nautičkog prometa mogu uzrokovati privremena napuštanja područja obitavanja, što je opisano u Kvarneriću (Rako i sur. 2013). Ovaj učinak ne mora nužno imati utjecaj na sve jedinke zajednice jer neke od njih mogu razviti određeni stupanj tolerancije (Wiszniewski i sur. 2010), što može objasniti relativno mali broj jedinki koje povremeno napuštaju područje obitavanja svoje zajednice (znanstveni rad **1**). Konačno, kao jedan od razloga povremenog napuštanja područja obitavanja navodi se pojačani pritisak predatora (Heithaus 2001). S obzirom da su u Jadranu opažanja vrsta koje su potencijalni predatori na dobre dupine izuzetno rijetka te da nikada nije potvrđena predacija, pritisak predatora se s velikom vjerojatnošću može isključiti kao razlog povremenih migracija zabilježenih u znanstvenom radu **1**.

Unatoč relativno malom broju jedinki opaženih izvan njihovog područja obitavanja (znanstveni rad **1**), one mogu imati značajnu ulogu za vijabilnost populacije dobrog dupina duž istočne obale Jadrana jer su nosioci važnih bioloških funkcija. Prema Papale i sur. (2016), ove jedinke smanjuju parenje u srodstvu (inbreeding) i time doprinose genskoj varijabilnosti, naročito u slučajevima malih i izoliranih lokalnih zajednica. Kod meta-populacija, ove jedinke omogućavaju re-kolonizaciju staništa u kojima je došlo do izumiranja prijašnje populacije

(Hanski i Gilpin 1991). Nadalje, one mogu biti vektori patogena (Lusseau i sur. 2006) i medijatori horizontalnog društvenog učenja (Mann i sur. 2012). Konačno, istraživanja ukazuju na to da prevaljivanje velikih udaljenosti kod određenih jedinki nisu izolirani slučajevi, već one to rade opetovano (Gnone i sur. 2011). Stoga te jedinke imaju trajnu funkciju povezivanja pojedinih zajednica čime doprinose koheziji i održavanju društvene strukture (Lusseau i Newman 2004).

Osim navedenog, disperzija je učestala kod mladih jedinki koje emigriraju iz natalnog područja i trajno naseljavaju druga područja. Kod sisavaca općenito vrijedi da je disperzija češća kod mladih mužjaka, dok ženke pokazuju natalnu filopatriju, odnosno privrženost području odrastanja (Greenwood 1980). U istraživanjima dobrih dupina, utvrđivanje natalne filopatrije je komplicirano radi činjenice da mlade jedinke u pravilu još nemaju prirodne oznake na temelju kojih ih se može foto-identificirati te je stoga praćenje tih jedinki kroz period odrastanja rijetko moguće. Stoga je i poznavanje disperzije mladih jedinki slabo poznato.

4.2. Čimbenici koji utječu na prostornu i društvenu strukturu

Drugi cilj ove disertacije, utvrđivanja čimbenika koji utječu na društvenu strukturu i područja obitavanja dobrog dupina, obrađen je u znanstvenom radu **2**. Ovo istraživanje provedeno je u području cresko-lošinjskog arhipelaga stoga što su u navedenom području dostupni podatci iz dužeg vremenskog razdoblja čime je omogućena analiza područja obitavanja na temelju jedinki opaženih 20 ili više puta, a što je skladu sa zahtjevima metode za što većim brojem opažanja (Seaman i sur. 1999). U navedenom području podatci su prikupljani tijekom cijele godine što je omogućilo analizu sezonskih varijacija čimbenika koji utječu na područja obitavanja.

Rezultati znanstvenog rada **2** ukazuju na spol jedinki kao najvažniji čimbenik s utjecajem na veličinu područja obitavanja i jačinu društvenih veza među jedinkama. Statistički značajno veća područja obitavanja kod ženki nego kod mužjaka, i to za sve metode procjene (MCP, KDE50 i KDE95), te za cijelu godinu i ljetni i zimski period zasebno, su rezultat suprotan rezultatima većine drugih istraživanja. Primjerice, foto-identifikacijom su veća područja obitavanja kod mužjaka nego kod ženki utvrđena u zaljevima Tampa (Urian i sur. 2009) i Sarasota (Owen i sur. 2002) na Floridi (SAD), dok i genetička istraživanja ukazuju na veću disperziju, posljedično i veća područja obitavanja, kod mužjaka (Wiszniewski i sur. 2010), što je slučaj i kod većine sisavaca (Möller i Beheregaray 2004). S druge strane, ovdje opažene razlike u područjima obitavanja između mužjaka i ženki u skladu su s istraživanjem od Gaspari i sur. (2013), čiji rezultati ukazuju na ženke kao glavne medijatore protoka gena u Jadranu. I drugdje u Jadranu postoje indikacije da ženke imaju veća područja obitavanja. U području otoka Visa utvrđeno je da neke ženke imaju veća područja obitavanja od mužjaka, ali statistički značajna razlika nije mogla biti potvrđena (Holcer 2012), dok su od jedinki poznatog spola koje su migrirale između područja obitavanja zajednica K i ND većina bile ženke (znanstveni rad **1**). Ipak, zbog činjenice da u oba slučaja nije moguće utvrditi spol svih opaženih jedinki, konačan zaključak nije moguće donijeti.

U cresko-lošinjskom arhipelagu veličina područja obitavanja kod mužjaka u korelaciji je sa stupnjem asocijacija među njima. Mužjaci sa najvišim stupnjevima asocijacija (> 0,9) bili su najčešće opažani i imali najmanja područja obitavanja (znanstveni rad **2**). Ovaj rezultat je u skladu s ranije opisanim slučajevima dugotrajnih „alijansi“ kod mužjaka dobrih dupina (Holcer 2012; Mann i sur. 2012), ali i drugih sisavaca (Amsler 2010). Prema Connor i sur. (1992) i Sprogis i sur. (2016), mužjaci formiraju alijanse jer kroz kooperaciju pospješuju pristup reproduktivnim ženkama. Posljedično, područja obitavanja alijansi variraju tijekom godine ovisno o reproduktivnom statusu ženki (Greenwood 1980; Clutton-Brock 1989) te su manja i uvjetovana prostornom distribucijom ženki u sezoni parenja (Sprogis i sur. 2016). No, iako je i u cresko-lošinjskom arhipelagu utvrđena sezona parenja tijekom ljeta (Bearzi i sur. 1997), mužjaci tada imaju veća područja obitavanja nego tijekom zime (znanstveni rad **2**). Stoga je samo reproduktivna strategija nedovoljna za objašnjavanje odnosa područja obitavanja mužjaka i ženki u cresko-lošinjskom arhipelagu.

Nadalje, rezultati znanstvenog rada **2** pokazuju da su razine stupnjeva asocijacija kod mužjaka uvjetovane intrinzičnim odabirom, a ne samom činjenicom da dijele zajednički prostor. Tako je kod ženki utvrđeno da je veličina preklapanja područja obitavanja među dvije jedinke u korelaciji sa stupnjem asocijacija među njima, dok kod mužjaka to nije slučaj. Zabilježeni su parovi mužjaka kod kojih je veličina preklapanja područja obitavanja velika, ali su društveno slabo povezani. Slučajevi gdje jedinke dijele prostor, ali su im razine društvenih interakcija niske zabilježeni su i drugdje, ali se dovode u vezu s drugim faktorima, a ne spolom. U Tršćanskom zaljevu (Genov i sur. 2019) i Australiji (Ansmann i sur. 2012) opisane su zajednice jedinki koje dijele prostor, ali imaju nizak stupanj interakcija. U oba istraživanja autori su utvrdili da su navedene zajednice društveno odvojene jer koriste drugačije strategije lova.

Pored intrinzičnih i antropogeni čimbenici imaju utjecaj na veličinu područja obitavanja dobrih dupina. Kao oni sa najviše utjecaja prepoznate su sezonske varijacije u intenzitetu nautičkog prometa te ribarstvo, odnosno koćarenje (znanstveni rad **2**). Neovisno o spolu i metodi procjene, jedinke u cresko-lošinjskom arhipelagu tijekom ljetnih mjeseci, odnosno za vrijeme značajnog povećanja broja plovila u području, imaju značajno veća područja obitavanja nego zimi (znanstveni rad **2**). Utjecaj nautičkog prometa na prostornu distribuciju dobrog dupina opisan je i ranije. Rako i sur. (2013) su u području Kvarnerića utvrdili da dobri dupini tijekom ljeta izbjegavaju one dijelove područja gdje je razina podvodne buke uslijed povećanog broja plovila najviša te im se relativne stope opažanja povećavaju u udaljenijim područjima s nižim razinama podvodne buke. Ovo za posljedicu ima i sezonsko povećanje područja obitavanja zabilježeno u ovome radu (znanstveni rad **2**). Sličan utjecaj nautičkog prometa zabilježen je i u zaljevu Shark (Australija) (Bejder i sur. 2006).

U cresko-lošinjskom arhipelagu zabilježene su značajne razlike u veličinama područja obitavanja jedinki u ovisnosti o tome jesu li uzete u obzir lokacije opažanja prilikom lova iza koćarica ili ne (znanstveni rad **2**). Utvrđeno je da mužjaci značajno češće primjenjuju ovu alternativnu strategiju lova nego ženke. Zadržavanje mužjaka u područjima gdje se koćari za posljedicu ima smanjenje njihovog područja obitavanja. Nasuprot tome, ženke za vrijeme brige o mladuncima izbjegavaju ovu tehniku lova, što Nelson (1990) i Fertl i Leatherwood (1997) objašnjavaju smanjenjem rizika od zapetljavanja. Ipak, koćarenje ima utjecaj na veličinu područja obitavanja oba spola tijekom ljetnih mjeseci kada i ženke pribjegavaju ovoj tehnici lova (znanstveni rad **2**). Ovo se dovodi u vezu sa činjenicom da ženke ljeti uslijed intenziviranog nautičkog prometa i s njim povezane razine podvodne buke napuštaju uobičajena područja lova te gubitak moraju nadoknaditi tehnikom lova iza koćarica.

I u drugim dijelovima Jadrana zabilježene su interakcije dobrih dupina s koćaricama, no postoje razlike u intenzitetu koćarenja i učestalosti interakcija među područjima. U Tablica 1 prikazana je usporedba intenziteta kočarenja iskazanog kao broj pregledanih koćarica po 100 km prijeđenog puta, te učestalost interakcija dobrih dupina s koćaricama iskazana kao postotak pregledanih koćarica koje su pratili dobri dupini. U sva tri navedena područja prisutnost dobrih dupina provjerena je kod svih opaženih koćarica u potegu te se stoga može smatrati da broj koćarica po 100 km prijeđenog puta predstavlja relativnu mjeru intenziteta koćarenja (Holcer 2012). Iz Tablica 1 vidljivo je da je relativni intenzitet koćarenja u području cresko-lošinjskog akvatorija više od dvostruko veći nego u području otoka Visa, i više od peterostruko veći nego u području sjeverne Dalmacije. Također, učestalost interakcija između koćarica i dobrih dupina je više od peterostruko viša u području cresko-lošinjskog arhipelaga nego oko otoka Visa i u sjevernoj Dalmaciji. Osim toga, u području otoka Visa nikada nisu zabilježene interakcije ženki s novorođenim mladuncima sa koćaricama, a na temelju podataka od ribara dobri dupini nikada ne prate koćarice u područjima dubljima od 100 m (Holcer 2012). Stoga je rezultate znanstvenog rada **2** nemoguće uopćiti za sva područja, već su potrebna daljnja istraživanja radi utvrđivanja mogućeg utjecaja koćarenja na područja obitavanja dobrih dupina u drugim dijelovima Jadrana.

Tablica 1. Usporedba intenziteta koćarenja i razina interakcija s dobrim dupinima među područjima u Jadranu.

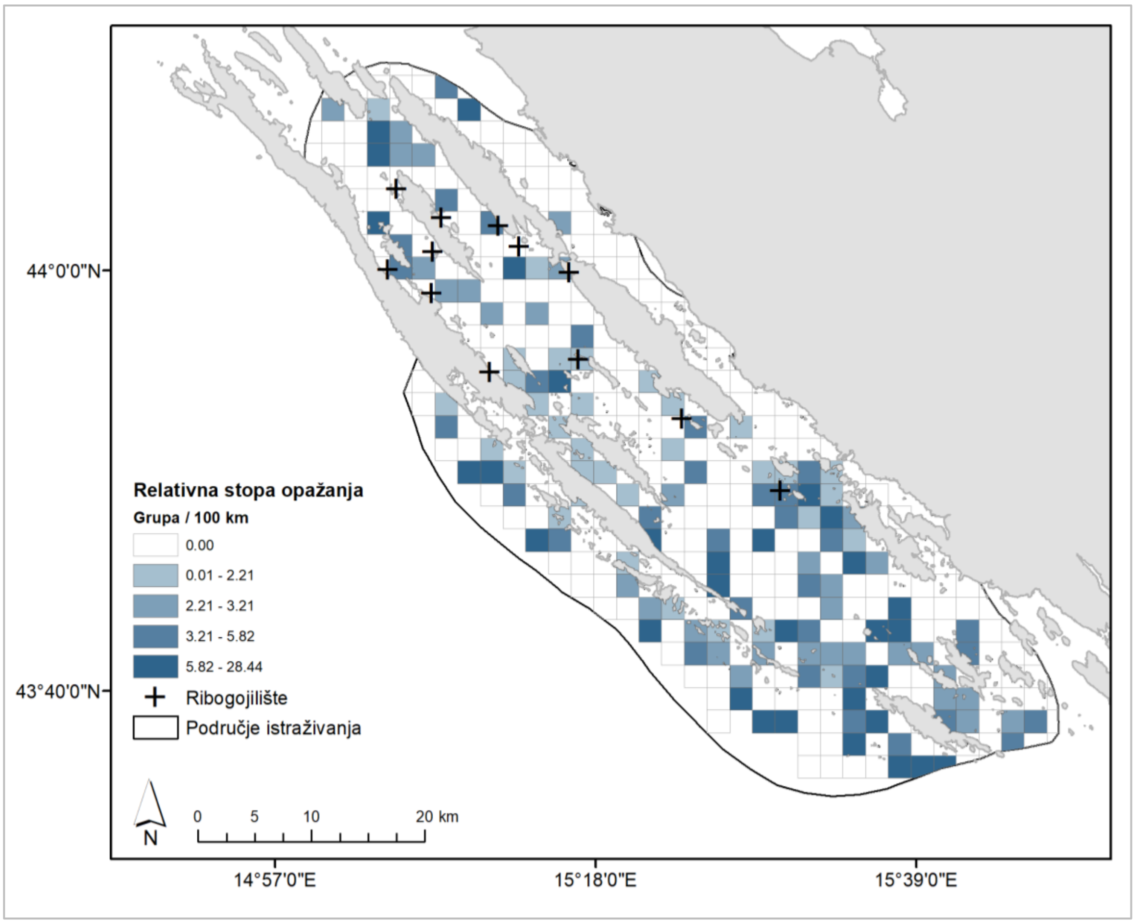
Područje	Cres-Lošinj	Sjeverna Dalmacija	Vis
Izvor	Znanstveni rad **2**	Znanstveni rad **3**	Holcer (2012)
Razdoblje	2005. – 2014.	2013. – 2017.	2007. – 2011.
Ukupno prijeđenih km	39693	13896	12610
Broj pregledanih koćarica	422	25	62
Broj koćarica po 100 km	1,06	0,17	0,49
Broj interakcija	100	1	16
Postotak interakcija	23,7 %	4 %	4,8 %

4.3. Dobri dupini u sjevernoj Dalmaciji

Kao dio ovog rada provedeno je prvo sustavno istraživanje dobrih dupina u području sjeverne Dalmacije (znanstveni rad **3**). Utvrđeno područje obitavanja zajednice u sjevernoj Dalmaciji (znanstveni rad **1**) korišteno je kao kriterij za odabir podataka za analizu demografskih parametara ove zajednice. Dobri dupini naseljavaju cijelo morsko područje sjeverne Dalmacije. Prosječna relativna stopa opažanja utvrđena za ovo područje kroz pet ljetnih sezona iznosi 1,5 grupa po 100 km prijeđenog puta, što je slično vrijednosti relativne stope opažanja utvrđenoj za područje Kvarnerića (1,6 grupa/100 km (Fortuna 2006)) i niže od one u području oko otoka Visa (2,5 grupa/100 km (Holcer 2012)). Također, vrijednosti relativne stope opažanja nisu se značajno razlikovale među godinama što upućuje na stabilnost prisutnosti dobrih dupina u navedenom području za trajanja ovog istraživanja. Vizualnim pregledom prostorne distribucije relativnih stopa opažanja moguće je utvrditi razlike u prisutnosti dobrih dupina unutar područja. Ovo je potvrđeno i Moranovim indeksom prostorne auto-korelacije (I = 0,081, z = 2,097, p = 0,036), koji ukazuje na to da dijelovi područja s višim relativnim stopama opažanja dobrih dupina nisu nasumični, već su u pozitivnoj korelaciji sa susjednim područjima. Relativne stope opažanja više su u blizini nekih ribogojilišta i općenito u jugo-istočnom dijelu područja dok su najniže u području Zadarskog i Pašmanskog kanala (Slika 2).

Ovakve razlike u prostornoj distribuciji i na relativno malom prostoru mogu biti uvjetovane raznim faktorima, od kojih se dostupnost plijena (Carnabuci i sur. 2016) i nautički promet (Rako i sur. 2013) ističu kao najvažniji. Više relativne stope opažanja u blizini ribogojilišta u skladu su s drugim istraživanjima (López i sur. 2005) i dovode se u vezu s povećanom koncentracijom plijena koji se tu okuplja zbog veće količine hrane. No, nemaju sva ribogojilišta u sjevernoj Dalmaciji jednak utjecaj na prisutnost dobrih dupina jer kod nekih (tri ribogojilišta uz otok Iž) dobri dupini nisu nikada opaženi tijekom pet ljetnih sezona. Stoga je potrebno istražiti kako pojedina ribogojilišta s obzirom na uzgajanu vrstu i faze uzgojnog ciklusa utječu na prostornu distribuciju dobrih dupina. Sjeverna Dalmacija ima razvijenu infrastrukturu nautičkog turizma (Kovačić 2012; Grcić 2015) što privlači veliki broj rekreacijskih plovila ljeti. Kako je ranije utvrđeno u Kvarneriću, dobri dupini ljeti izbjegavaju područja s najvećom koncentracijom rekreacijskih plovila i posljedično najvišom razinom podvodne buke (Rako i sur. 2013), a sličan utjecaj može se očekivati i u sjevernoj Dalmaciji. Radi boljeg razumijevanja utjecaja antropogenih čimbenika na prisutnost i prostornu distribuciju dobrih dupina u sjevernoj Dalmaciji potrebna su daljnja istraživanja koja će uključiti modeliranje načina korištenja staništa u ovisnosti o lokacijama, vrsti i uzgojnom ciklusu ribogojilišta, vrsti i intenzitetu brodskog prometa te lokacijama od značaja za nautički turizam (urbana središta, marine, pomorske benzinske postaje).

Prema učestalosti opažanja u sjevernoj Dalmaciji, 53,3 % jedinki opaženih tijekom dvije ili više ljetnih sezona može se smatrati rezidentnima. Od preostalih 46,7 % jedinki opaženih tijekom jedne ljetne sezone, njih 71,4 % opaženo je samo jednom što upućuje na kratkotrajan boravak ovih „tranzijentnih“ jedinki u području istraživanja i u skladu je sa rezultatima analiza stopa migracija među područjima obitavanja (znanstveni rad **1**). U Jadranu, sličan omjer rezidentnih i tranzijentnih jedinki pronađen je u području otoka Visa (47 %) (Holcer 2012), dok je u Tršćanskom zaljevu udio tranzijentnih jedinki viši (57 %) (Genov i sur. 2008).



Slika 2. Prostorna distribucija relativnih stopa opažanja dobrog dupina u sjevernoj Dalmaciji, na kvadratnoj mreži duljine stranica od 2 km.

U području sjeverne Dalmacije brojnost dobrih dupina, procijenjena modelom otvorene populacije i na temelju uzorka jedinki opaženih dva ili više puta, varira kroz pet ljetnih sezona između 116 jedinki u 2016 godini (95 % CI = 107-133) i 138 jedinki u 2015 godini (95 % CI = 121-165), no razlike među godinama nisu statistički značajne. Također, regresijska krivulja ukazuje na pad brojnosti od 11,4 % tijekom 5 godina, no ovaj pad nije statistički značajan. Izostanak statistički značajnih razlika u brojnosti, ali i prosječnim veličinama skupina kao i relativnim stopama opažanja kroz vrijeme (znanstveni rad **3**) ukazuje na to da područje sjeverne Dalmacije naseljava relativno mala, ali stabilna zajednica dobrih dupina.

U drugim dijelovima Jadrana, brojnost dobrih dupina procijenjena je na otprilike 200 jedinki u cresko-lošinjskom arhipelagu (Pleslić i sur. 2015), 69 jedinki u tršćanskom zaljevu (Genov i sur. 2008), otprilike 350 jedinki u području otoka Visa (Holcer 2012), te na 90 jedinki u moru Crne Gore (Miočić-Stošić i sur. 2020). No, treba naglasiti da se navedene procjene brojnosti odnose na područja istraživanja određena logističkim ograničenjima, a koja ne odražavaju nužno stvarno područje obitavanja lokalnih zajednica, za razliku od znanstvenog rada **3** u kojem je područje istraživanja određeno temeljem poznavanja područja obitavanja lokalne zajednice (znanstveni rad **1**). Stoga je umjesto direktne usporedbe procijenjenih brojnosti primjerenija usporedba gustoća kao jednostavnih omjera procijenjenog broja jedinki i površine područja istraživanja (Tablica 2). Ovom usporedbom gustoća dobrih dupina u sjevernoj Dalmaciji slična je onima u Tršćanskom zaljevu i u akvatoriju otoka Visa, te nešto viša od one u moru Crne Gore. Gustoća u navedenim područjima je više nego dvostruko niža od one u cresko-lošinjskom arhipelagu. Ove razlike mogu ukazivati na stanje okoliša, odnosno kapacitet za održavanje većeg ili manjeg broja jedinki dobrih dupina (Davis i sur. 2002). Stoga su potrebna daljnja istraživanja radi utvrđivanja veza između stanja okoliša i veličine lokalnih zajednica dobrih dupina.

Tablica 2. Usporedba gustoća dobrih dupina između područja istraživanja u Jadranu.

Područje	Površina (km^2)	Procijenjena brojnost	Gustoća (brojnost/km^2)	Izvor
Sjeverna Dalmacija	2500	125	0,05	Znanstveni rad **3**
Cres-Lošinj	1600	199	0,12	(Pleslić i sur. 2015)
Vis	7400	348	0,04	(Holcer 2012)
Tršćanski zaljev	1200	70	0,05	(Genov i sur. 2008)
Crna Gora	2600	90	0,03	(Miočić-Stošić i sur. 2020)

Osim brojnosti, za potpuno poznavanje stanja i predviđanje budućih demografskih trendova lokalnih populacija ili zajednica potrebne su informacije o stopama preživljavanja po spolu i dobnim skupinama te o reprodukcijskim parametrima (Vermeulen i Brager 2015). Znanstvenim radom **3** procijenjene su stope preživljavanja za odrasle jedinke i mladunce te je određena stopa okota za zajednicu dobrih dupina u području sjeverne Dalmacije. Procijenjene stope preživljavanja za odrasle jedinke u sjevernoj Dalmaciji u pravilu su bile iznad 0,9. Ovako visoke stope preživljavanja odraslih jedinki očekivane su kod dugoživućih vrsta. U području Kvarnerića u razdoblju od 1997. do 2003. stope preživljavanja odraslih jedinki procijenjene su na više od 0,9 (od 0,914 do 0,938) u svim godinama osim 1999. (0,825) (Fortuna 2006). I u drugim područjima stope preživljavanja odraslih jedinki procijenjene su na preko 0,9: u regiji

Fiordland (Novi Zeland) (Currey i sur. 2009), u zaljevu Shark Bay (Australija) (Nicholson i sur. 2012), u zaljevu San Matias (Argentina) (Vermeulen i Brager 2015), kod Pertha (Australija) (Chabanne i sur. 2017) i u zaljevu Walvis (Namibia) (Elwen i sur. 2019). I kod mladunaca je procijenjena stopa preživljavanja do prve godine života (0,875) slična onima procijenjenima u zaljevu Sarasota (SAD) (0,803) (Wells i Scott 1990), regiji Firodland (Novi Zeland) (0,862) (Currey i sur. 2009) i zaljevu Moray Firth (Škotska) (0,865) (Wells i Scott 1990; Currey i sur. 2009; Arso Civil i sur. 2018), te viša od one procijenjene za područje Kvarnerića (0,771) (Fortuna 2006). Poznavanje ovih parametara omogućiti će daljnje praćenje stanja ove zajednice radi utvrđivanja mogućih trendova, ali i analizu vijabilnosti zajednice za duži vremenski period.

Reprodukcijske značajke kod ženki naročito su važne za one populacije poligamnih vrsta kod kojih ukupna dostupnost mužjaka ne ograničava mogućnost parenja (Caswell 2000). U ovome radu omjer spolova u ukupnom uzorku u području sjeverne Dalmacije nije bilo moguće odrediti jer kod dobrih dupina ne postoji spolni dimorfizam. Stoga su godišnje stope okota utvrđene samo na uzorku jedinki koje su mogle biti određene kao ženke na temelju opetovanih opažanja sa mladuncima (znanstveni rad **3**). Stopa okota varirala je među godinama, od 0,02 do 0,23, uz prosjek od 0,17 i standardnu pogrešku od 0,04 . U Jadranu, koristeći jednaku metodu, jednaka stopa okota zabilježena je u cresko-lošinjskom arhipelagu (Fortuna 2006), dok je u području oko otoka Visa ona nešto niža i iznosi 0,14 (Holcer 2012). Drugdje u svijetu, gdje su ove procjene izrađene istom metodologijom, zabilježene su varijabilne godišnje stope okota. Tako u zaljevu Islands (Novi Zeland) one variraju godišnje od 0,25 do 0,32 (Tezanos-Pinto 2009), u Ligurskom moru od 0,29 do 0,41 (Rossi i sur. 2017), dok u Škotskoj iznose 0,11 (Mitcheson 2008), u Patos laguni (Brazil) 0,11 (Fruet i sur. 2015) i u zaljevu Sarasota (SAD) 0,14 (Wells i Scott 1990). Treba naglasiti da su ovdje navedene stope okota procijenjene temeljem podataka o opaženim i uspješno foto-identificiranim jedinkama, a koji ne obuhvaćaju nužno sve okote u populaciji u pojedinoj godini. Stoga su stvarne stope okota više. Tako su Cheney i sur. (2019) korištenjem modela procjene koji uzima u obzir neopažene okote procijenili više stope okota (0,23) nego korištenjem tradicionalne metode (0,14) za istu populaciju i vremensko razdoblje.

4.4. Metapopulacija i zaštita

Sagledavajući sve rezultate ovog istraživanja, preostaje pitanje može li se populacija dobrog dupina uz istočnu obalu Jadrana okarakterizirati kao meta-populacija? Originalna definicija meta-populacije od Levins (1970), koja podrazumijeva da lokalne populacije nestaju i nastaju, ovdje nije primjenjiva. Kod dugoživućih vrsta, poput dobrog dupina, potrebno je više desetljeća istraživanja kako bi se mogli potvrditi ili odbaciti procesi ekstinkcije lokalne populacije i uspostave nove populacije priljevom jedinki iz nekog drugog područja. Kod ove vrste, jedini poznati slučaj izumiranja lokalne populacije (zajednice) i ponovnog naseljavanja opisan je u ušću rijeke Humber (Engleska) temeljem DNK analize (Nichols i sur. 2007). Izuzimajući uvjet da se mogu potvrditi ekstinkcija i re-kolonizacija, pojam meta-populacije dobro opisuje strukturu populacije dobrog dupina uz dio istočne obale Jadrana obuhvaćen ovim radom jer su pronađeni neki od ostalih elemenata koje ova definicija obuhvaća. Naime, prema Grimm i sur. (2003), prostorno strukturiranje populacije kakvo je zabilježeno u ovom radu (znanstveni rad **1**) osnovni je kriterij za definiciju meta-populacije u morskom staništu. Također, utvrđeno je da su lokalne populacije (zajednice) u međusobnom kontaktu kroz jedinke koje migriraju među njihovim područjima obitavanja (znanstveni rad **1**), dok rad od Gaspari i sur. (2013) ukazuje na to da ženke vrše funkciju medijatora gena među različitim područjima. Ipak, iako su pronađene neke razlike u parametrima populacijske dinamike između zajednica Kvarnerića (Fortuna 2006; Pleslić i sur. 2015), sjeverne Dalmacije (znanstveni rad **3**) i Visa (Holcer 2012), potrebna su daljnja istraživanja kako bi se utvrdilo da li nekoj od zajednica prijeti ekstinkcija i da li su natalitet i mortalitet ovih zajednica međusobno neovisni, što bi ih okarakteriziralo kao lokalne populacije u meta-populaciji.

Bez obzira na to koliko, prema postojećim spoznajama, struktura populacije dobrog dupina uz istočnu obalu Jadrana odgovara definiciji meta-populacije, ovaj pojam je i dalje koristan kao idejni okvir jer upućuje na važna pitanja za daljnja istraživanja. U ovom slučaju, buduća istraživanja potrebno je usmjeriti ka priobalnim područjima koja do sada nisu obuhvaćena (istarski akvatorij te područja jugo-istočno od Lastova) te razumijevanju uloge koju tranzijentne jedinke iz otvorenog dijela Jadrana imaju u populacijskoj dinamici priobalnih zajednica. Nadalje, istraživanje genetičke strukture populacije dobrih dupina u sprezi sa daljnjim foto-identifikacijskih istraživanjima omogućilo bi bolje razumijevanje strukture i dinamike cijele populacije dobrih dupina u istočnom Jadranu. Rezultati ove disertacije predstavljaju osnovu za takva istraživanja i daljnje praćenje stanja populacije dobrog dupina, što je obaveza država članica EU temeljem Članka 11 Direktive o zaštiti prirodnih staništa i divlje flore i faune (EEC92/43).

Konačno, rezultati ove disertacije i sagledavanje populacije dobrog dupina duž istočne obale Jadrana kao meta-populacije nose implikacije za zaštitu ove vrste. Dobri dupin je u

Hrvatskoj zaštićen na temelju Zakona o zaštiti prirode (NN14/19 ; NN15/18 ; NN80/13 ; NN127/19), dok je na razini Europske unije kao ciljna vrsta za zaštitu naveden u Dodatku II i Dodatku IV Direktive o zaštiti prirodnih staništa i divlje flore i faune (EEC92/43). U Republici Hrvatskoj dobri dupin je ciljna vrsta za očuvanje u šest Područja očuvanja značajnih za vrste i stanišne tipove (POVS) koja su dio Natura 2000 ekološke mreže (NN80/2019). Od toga, četiri POVS područja nalaze se gotovo u cijelosti unutar područja obitavanja tri opisane zajednice (znanstveni rad **1**; Slika 10). Rezultati ove disertacije direktno doprinose ispunjavanju dva od četiri kriterija iz Dodatka III Direktive o staništima za ocjenu važnosti POVS područja: kriterij B.a. koji zahtjeva procjenu veličine i gustoće populacije vrste koja je prisutna na području ekološke mreže u odnosu na populacije prisutne na teritoriju cijele države (Znanstveni rad **3**) te kriterij B.c. koji zahtjeva procjenu stupnja izoliranosti populacije koja je prisutna na području ekološke mreže u odnosu na prirodnu rasprostranjenost vrste (Znanstveni rad **1**).

Osim toga, rezultati ove disertacije, odnosno primjena koncepta meta-populacije pri izradi planova upravljanja, koji trenutno ne postoje ni za jedno od šest Natura 2000 područja namijenjenih zaštiti dobrog dupina u Jadranskom moru, omogućavaju izradu mjera zaštite prilagođenih zasebnim zajednicama te time i zaštiti cijele meta-populacije. Čimbenici koji mogu negativno utjecati na status zaštite dobrih dupina nisu jednakomjerno prisutni u prostoru i vremenu dok zajednice, ovisno o demografskim značajkama, mogu različito reagirati na te čimbenike. Primjerice, udio slučajeva namjernog ubijanja i slučajnog ulova u ribarske alate (oboje zabilježeno u znanstvenom radu **3**) u ukupnoj stopi mortaliteta zajednica može se razlikovati među područjima ili biti nepoznat. U malim i izoliranim populacijama (zajednicama) čak i male varijacije demografskih značajki, uzrokovane prirodnim ili antropogenim čimbenicima, mogu značajno povećati rizik od izumiranja (Goodman 1987) dok su velike populacije otpornije na takve varijacije (Lacy 1993). Iz tog razloga mjere zaštite trebaju biti izrađene za svako područje zasebno, uzimajući u obzir razlike u vrsti i intenzitetu prijetnji (na primjer Tablica 1) kao i razlike u demografskim značajkama zajednica prisutnih u navedenim područjima.

5. ZAKLJUČCI

1. Populacija dobrog dupina uz istočnu obalu Jadrana strukturirana je u najmanje tri društvena klastera. Stupnjevi asocijacija među jedinkama istog klastera značajno su viši od stupnjeva asocijacija među jedinkama iz različitih klastera. Osim toga, procijenjena područja obitavanja tri klastera se ne preklapaju. Stoga se tri navedena klastera mogu smatrati lokalnim zajednicama prema definiciji od Croft i sur. (2008).

2. Relativno nizak broj jedinki prelazi iz područja obitavanja jedne zajednice u područje obitavanja druge, odnosno stupanj migracije uzduž obale je nizak. Također, ovi prelasci jedinki u područja obitavanja susjednih zajednica su rijetki i kratkotrajni. U područjima obitavanja identificiranih lokalnih zajednica utvrđen je relativno visok broj jedinki opaženih samo jednom, a koje nisu opažene u područjima obitavanja drugih lokalnih zajednica. Ovo upućuje na to da lokalne zajednice nisu izolirane i da se glavnina migracija događa između područja otvorenog mora koje nije obuhvaćeno istraživanjem i područja obitavanja priobalnih lokalnih zajednica identificiranih u ovoj disertaciji.

3. Najznačajniji čimbenici koji utječu na područja obitavanja jedinki dobrog dupina su spol, stupnjevi asocijacija te ljudske aktivnosti uključujući ribarstvo i nautički promet.

4. Utvrđeno je da ženke imaju statistički značajno veća područja obitavanja od mužjaka. Također je utvrđeno da ženke imaju veća područja obitavanja dok imaju mladunče, no ova razlika nije bila statistički značajna. Područja obitavanja mladunaca nakon osamostaljenja preklapaju se s onima njihovih majki što upućuje na natalnu filopatriju.

5. Statistički značajne razlike u veličini područja obitavanja za oba spola utvrđene su usporedbom ljetnih i zimskih mjeseci te usporedbom podataka prikupljenih tijekom opažanja dupina prilikom lova iza koćarica sa ostalim podatcima. Utvrđeno je da oba spola tijekom ljetnih mjeseci, kada je nautički promet značajno pojačan, imaju veća područja obitavanja. Tijekom ljetnih mjeseci, oba spola značajno češće koriste lov iza koćarica u područjima udaljenim od obale, odnosno gdje je nautički promet slabiji, što dodatno utječe na povećanje područja obitavanja tijekom ljetne sezone.

6. Stupnjevi asocijacija među ženkama bili su značajno niži nego među mužjacima. Također, statistički značajna korelacija između stupnjeva asocijacija i stupnjeva

preklapanja područja obitavanja utvrđena je jedino kod ženki. Ovo je u skladu sa činjenicom da ženke imaju veća područja obitavanja od mužjaka i fluidniju društvenu strukturu, dok mužjaci formiraju čvršće društvene veze s manjim brojem drugih mužjaka i pokazuju izraženiju teritorijalnost.

7. U razdoblju od 2013. do 2017. godine utvrđene su godišnje varijacije brojnosti lokalne zajednice dobrog dupina u sjevernoj Dalmaciji od 116 jedinki u 2016. godini do 138 jedinki u 2015. godini. Godišnje stope opažanja u ovom području variraju od 1,16 skupina po 100 km u 2014 godini. do 1,94 skupine po 100 km u 2015 godini. S obzirom da statistički značajan trend u brojnosti i stopama opažanja nije utvrđen, zajednica dobrog dupina u sjevernoj Dalmaciji može se smatrati relativno malom, ali stabilnom.
8. Osim lokalne zajednice, područje sjeverne Dalmacije koriste i jedinke koje dolaze iz otvorenog dijela Jadranskog mora, a koje sačinjavaju 46,7 % ukupno identificiranih jedinki u ovom području. Također, godišnja stopa emigracije procijenjena za lokalnu zajednicu u području sjeverne Dalmacije iznosi 0,172. Stoga se ova zajednica može smatrati otvorenom.
9. U području sjeverne Dalmacije utvrđene su prosječne veličine skupina od 5,73 jedinki u 2015. godini do 7,46 jedinki u 2017. godini, no bez statistički značajnih razlika među godinama. Statistički značajne razlike pronađene su između veličina skupina sa mladuncima i skupina bez mladunaca.
10. Procijenjene godišnje stopa preživljavanja odraslih jedinki u sjevernoj Dalmaciji su više od 0,9, dok je godišnja stopa preživljavanja mladunaca do prve godine starosti procijenjena je na 0,875. Ovi rezultati su u skladu sa drugim istraživanjima ove vrste i očekivani kod dugoživućih vrsta.
11. Godišnja stopa okota u sjevernoj Dalmaciji iznosi 0,17.
12. S obzirom na utvrđenu prostornu i društvenu strukturiranost, relativno niske stupnjeve interakcija među jedinkama utvrđenih zajednica i razlike u demografskim parametrima lokalnih zajednica, može se smatrati da pojam meta-populacije dobro opisuje strukturu populacije dobrog dupina u području istraživanja.

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7. ŽIVOTOPIS AUTORA

Grgur Pleslić rođen je 17.7.1980. u Zadru gdje pohađa osnovnu školu i gimnaziju Vladimira Nazora. Nakon mature kratko studira na Fakultetu strojarstva i brodogradnje u Zagrebu, no veći interes pronalazi u prirodnim znanostima te prelazi na Prirodoslovno-matematički fakultet u Splitu gdje studira biologiju i kemiju. Već prije završetka studija zapošljava se u Institutu za istraživanje i zaštitu mora Plavi svijet u Velom Lošinju gdje godinu dana radi u programu edukacije nakon čega prelazi u program istraživanja. Od tada aktivno sudjeluje u svim znanstveno-istraživačkim projektima Instituta Plavi svijet. Znanstveni interes fokusiran mu je na prostornu ekologiju, modeliranje populacijskih parametara temeljem „mark-recapture“ podataka te analizu društvenih mreža kod dobrog dupina. Osim toga, sudjeluje i u drugim disciplinama uključujući istraživanje velikih morskih kralježnjaka iz zraka, istraživanje ponašanja i interakcija dobrog dupina sa ribarstvom te aktivno radi i na moderniziranju metode foto-identifikacije i primjeni najnovijih programskih rješenja u automatizaciji procesa prikupljanja i obrade podataka, te razvoju programa građanske znanosti. Pored rada u istraživačkom programu sudjeluje i u izradi i upravljanju projektima.

Obrazovanje

1999 – 2010 Prirodoslovno-matematički fakultet, Split. Smjer biologija i kemija

Radno iskustvo

2020 – 2021 Institut Plavi svijet – Direktor znanstvenog programa

2013 – 2019 Institut Plavi svijet – Voditelj istraživanja

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